The Journal of HEREDITY

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Dwarf Jersey Cattle

Six Generations Per Century

Efficiency of Selection Methods

Biological "Facts" for The Sociologist

A New Salivary Gland Chromosome Map

Association of Temperament and Coat Color in the Rat

VOLUME 33 NOVEMBER, 1942 NUMBER 11

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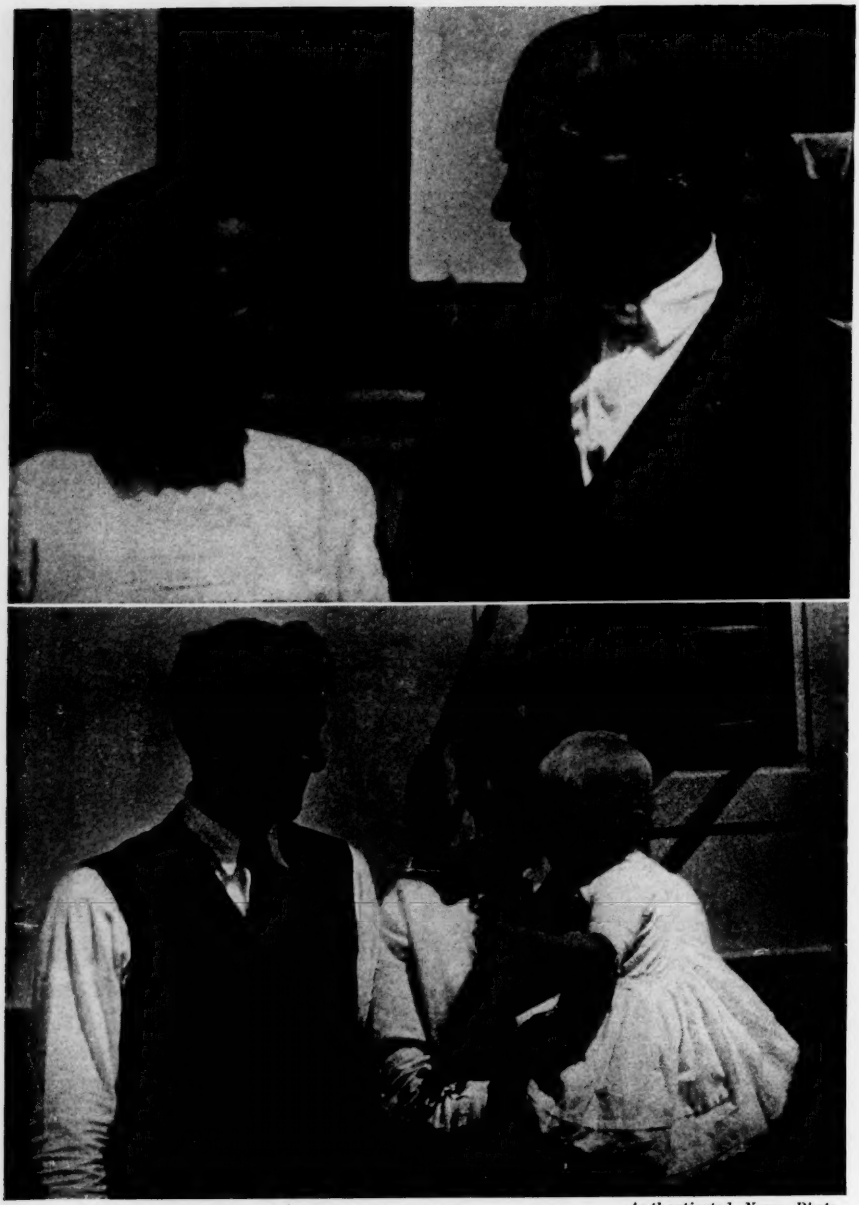

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SIX GENERATIONS TO A CENTURY

Figure 1

A mother during her fifteenth year, and a grandmother at 29, Maria Mlinaric might have over a thousand great-great-great-great-grandchildren by the year 2000. See page 408.

THE ASSOCIATION OF THE BLACK (non-agouti) GENE WITH BEHAVIOR

In the Norway Rat

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IN a paper presented before the American Society of Zoologists in Dallas December 1941 there was given a general account of what were interpreted as the pleiotropic effects of certain coat-character genes upon morphology and behavior.[1]

In that preliminary report evidence was presented to show that in certain crosses of the Norway rat there was a definite association between coat color genes and temperament. These crosses were between albino rats of the Wistar strain, which carry black, and wild gray Norway rats. In the coat color segregates in F_2 and later generations it was found that the rats carrying the black gene tended to be tamer and less aggressive than the gray segregates. The observations there reported have been supplemented and new tests have been applied to assay the temperamental differences, so that the findings are now based on a large enough body of data to have unquestionable statistical significance.

The question of whether these temperamental differences are due to the pleiotropic effects of the actual coat color gene, or to the close linkage of that gene with distinct temperament genes is not completely settled by the data here presented. The writer is inclined to believe that pleiotropy rather than linkage accounts for these effects. Evidence favoring pleiotropy of the taming effect associated with the black (non-agouti) gene rather than linked-genes is as follows:

1. Of the tame laboratory strains of Norway rats in America, it was learned mainly by correspondence that the following contain the black gene: August 990 (by mutation), Fischer 6, Fischer 230, Fischer 344, King Inbred, Marshall 520, McCollum, New Haven, Osborne-Mendel, Philadelphia, Riddle, Curtis-Dunning selfed 34069, Sherman, Sprague-Dawley, Wistar Albino, Wistar Piebald, Yale, Zimmerman 61. Although these strains (except August 990) may possibly trace their black genes to the same mutation a hundred or more years ago, because most laboratory strains are distantly related, still these strains must have provided in recent years a great variety of residual hereditary backgrounds upon which to display the probable behavior tendencies of the black gene. Some of the strains named above have independent origins. Some are descended from Wistar Albinos; some from the Osborne-Mendel group. But because both of these source strains had mixed origins, it appears that some opportunity has been given originally for separating the black gene from any possible linked taming gene. The same applies to the August 990 strain during its origin. An additional black strain is said by Dunning to be wild, but whether the wildness here is due to linked genes or to other genetic changes cannot be determined except by a long breeding program.

2. A survey of stocks at the Wistar Institute revealed the fact that two black strains were derived by King from outcrosses of tame albino (carrying black) to wild gray Norway. These black strains were tame. Another strain of tame blacks was derived from a mixture of segregates from several outcrosses of different strains containing black. It is known that Hatai (1914) made an outcross of tame Wistar Albinos (carrying black) to wild gray Norway rats. From this cross there descended a self black and a black hooded strain. The black hooded strain exists today, and is tame.

The black strain is extinct, but is reported verbally by members of the Wistar staff to have been tame.

The Lashley and the Long-Evans strains arose from similar outcrosses of tame albinos carrying black, to gray Norway. Castle (personal communication) has examined a pair of black rats from the Long-Evans strain and reports them "well behaved." Enders (personal communication) finds his black hooded derivatives of Lashley's cross to be tame.

Each of the above named crosses gave opportunities for crossing-over between the black gene and possible, linked, tameness genes if such had been present.

3. Because King's mutant black stock was derived from the recessive black individuals that segregated from her gray Norways during at least four consecutive generations, there were many opportunities in five or more generations for crossovers between the recessive black gene in heterozygous state and any possible linked taming gene or genes. Today, tame black mutants are segregating from the 56th generation of gray Norways. One adult black segregate has been examined and found to be tame as compared with its gray siblings. If this is a continued segregation of the old black mutation, rather than of a new mutation to black, there have been manifold opportunities for crossing over in at least 44 generations on the linked gene assumption. If a new mutation, there must be assumed the simultaneous mutation of at least one linked tameness gene, unless we accept the pleiotropy hypothesis. At least 25 of the earlier black segregates from the King gray strain have come under the observation of several persons, who describe them all as tame by nature. No black mutants were observed to be wild.

4. King has a strain of chocolate rats derived from Cinnamon plus black (non-agouti). They are tame. Castle has made crosses with some of these animals and states (personal communication) that chocolate segregates are in general tame, whereas cinnamons may be wild. Hence it would appear that the taming effect associated with the black gene in duplex can overcome the wilding effects not only of the gray Norway background, but also of the gray Norway background plus the cinnamon gene in duplex.

The present paper also bears out the foregoing lines of evidence, in that marked behavior differences appear between black (non-agouti) and gray Norway rats segregating from a cross of wild gray Norway to tame Wistar albinos.* This study, unlike the earlier one based on impressionistic observations[1] utilizes certain simple behavior tests for the purpose of recording individual responses to definite situations. Such responses could be subjected to mathematical checks for the statistical significance of such differences in behavior as might be correlated with black and gray coat colors respectively.

Materials

Three Wistar albino females were mated to a gray Norway male, and hence it may be assumed that in the hybrids to be described, we are always dealing with the same identical black gene.

Wistar albinos are homozygous for the three independent Mendelian recessive coat-character genes: albino, hooded (piebald) and black. Because these genes are all recessive (hooded giving in simplex a white belly spot, white paws and white tail tip) nothing except grays hybrid for all three recessive genes are obtained in the first hybrid generation. When a second hybrid generation is produced by crossing together members of the first hybrid generation a normal, trihybrid, mendelian ratio is obtained of theoretically 27 grays, 9 albinos, 9 hooded, 9 black, 3 albino hooded, 3 albino-black, 3 black hooded, and 1 albino-black-hooded. In such a segregation there will be homozygous grays and grays ranging from those hybrid for any one up to all possible combinations

*Blacks and grays were chosen for intensive study because these two color-groups gave the most clear-cut distinctions of any of the color-groups reported upon previously by Keeler and King.[1]

of the three recessive characters. Albinos may carry one gene or two genes for any or all of the possible combinations of coat characters or they may carry none of them. The blacks, on the contrary, cannot carry the gene for gray, although they may carry a gene for albinism without detection.

Thus, albinos will be useless for comparisons, and grays will be expected to be more variable than blacks in behavior.

One hundred and twenty-five F_2 and backcross segregates (heterogeneous as to color), derived from the cross described above, were available. These have been subjected individually to several tests such as those listed by Hall.[2] The results of these tests may be compared by color classes.

The test segregates have been raised with animals of the several color varieties confined in the same cages. It is now realized, however, that there are possible advantages in raising each coat-color class separately for the purpose of revealing all the inborn behavior differences existing between color classes, because of the probable environmental influence of cage associates upon behavior of the individual.

It may also be mentioned that sexes were separated, and about the same number of rats were kept in each cage because of the taming effect of crowding and the wilding effect of few associates or solitude. The average number of rats to a Wistar cage was five. Segregates were not handled from the time of weaning on, nor were they allowed to become previously familiar with the observer, in order that maximum differences could be obtained in the adults.

We might expect the first test on segregates to be the most significant, because even wild rats become tamer with handling and soon are accustomed to a particular observer, as is evidenced by the holding experiments about to be described. Indeed, they probably become tame and docile in the hands of a particular observer long before they may be handled by others.

It may be stated that the hybrid rats of this series had become accustomed to the presence of persons in the laboratory although they had not been handled. As a group, they gnawed their cages very much, as do wild grays and mutant albinos, in contrast to all other strains in the laboratory. This fact is an indication of their greater average activity.

First Holding Test

For the first holding test the door of each cage was opened and a rat was

TABLE I. First Holding Test.*

Color of Segregates	Gray	Albino	Gray Hood	Gray + Gray Hood	Black	Black Hood	Black + Black Hood	Significance Gray vs Black
Number of Rats	45	28	22	67	23	7	30	
% Biting	34	28	45	40	13	0	10	hs
% Attacking	4	14	18	9	4	0	3	–
% Squealing	67	71	73	68	39	28	37	hs
% Opening Mouth	0	0	4	1	0	0	0	–
% Laying Ears Back	49	18	36	45	9	1	10	hs
% Puffing	7	17	18	10	0	0	0	–
% Whining	17	10	18	18	4	2	10	x
% Chittering	2	7	18	18	4	0	3	x
% Urinating	53	46	45	51	9	0	7	hs
% Defecating	73	75	64	70	43	57	47	s
% No Reaction	2	7	0	1	30	28	30	hs
Av. No. Reactions	3.11	2.75	3.41	3.22	1.26	1.28	1.27	

*The significance of differences in reaction between gray and gray hooded vs. black and black hooded rats recorded in the tables, has been determined through the kindness of Prof. H. M. Lufkin using Fisher's chi-square method. Chances less than .05 and greater than .01 (following Snedecor) are considered significant (marked *s*). Chances less than .01 are highly significant (marked *hs*) and those greater than .90 have no significance (marked *x*).

The method used for determining the significance of differences between the means for reactions consists of first setting up a fourfold table of coat color against frequences of reactions and non-reactions. The value of chi-square is obtained for one degree of freedom, and with Yates' correction applied. Fisher feels that this is more satisfactory than the use of the point-binomial. (See Fisher and Yates,[4] p. 3.)

taken at random in the observer's heavily gloved hand. As little commotion as possible was caused. The animal was withdrawn from the cage and held quietly in the hand for one minute during which time a number of possible reactions were counted that are recorded in Table I.

For purposes of comparison the albinos are of little value, because we do not know which individuals carry and which do not carry black latently, as mentioned above. Because we are really desirous of comparing merely the differences between animals bearing two doses of the black gene and ones bearing its gray allel homozygously or heterozygously, we have combined grays with gray hoodeds and blacks with black hoodeds. Here we find the grays have a higher score than the blacks for biting (40:10%), attacking (9:3%), squealing (68:37%), opening mouth (1:0%), laying ears back (45:10%), puffing (10:0%), whining (18:10%), chittering (18:3%), urinating (51:7%), defecating (70:47%). One per cent of grays and gray hoodeds gave no reaction against 30% for blacks and black hoodeds. The average number of reactions per individual was 3.22 for grays and 1.27 for blacks. When these figures are examined statistically it is found that the differences in response for blacks and grays are highly significant for biting, squealing, laying ears back, urinating and no reaction. The difference is also significant for defecating.

The above described observations were made on February 16. An annoyance test was carried out by nose-tickling with brush bristles on March 2. Two emergence tests were conducted on March 3 and March 4 respectively. Then a second holding test was made on March 5. This time the blacks and black hoodeds were removed last from each cage, it being supposed that the commotion of removing the grays might change their recognized tame behavior. However, the differences between blacks and grays have not been eliminated entirely as will be seen in Table II.

TABLE II. Second Holding Test.

Color of Segregates	Albino	Gray	Gray Hood	Gray + Gray Hood	Black	Black Hood	Black + Black Hood	Significance Gray vs. Black
Number of Rats	28	45	22	67	23	7	30	
% Biting	7	20	18	19	9	0	7	x
% Attacking	0	11	0	7	4	0	3	x
% Squealing	18	55	27	46	35	28	30	x
% Opening Mouth	0	2	0	1	0	0	0	–
% Laying Ears Back	7	60	0	40	17	0	13	hs
% Puffing	3	9	5	7	0	0	0	–
% Whining	14	9	0	6	9	71	23	x
% Chittering	0	4	5	4	0	28	7	x
% Urinating	32	47	32	42	30	14	27	x
% Defecating	50	47	27	40	69	43	63	s?
% No Reaction	11	4	9	6	9	14	10	x
Av. No. Reactions	1.32	2.64	1.14	2.15	1.74	1.86	1.77	

Second Holding Test

Grays and gray hoodeds combined still exceed blacks and black hoodeds in the second holding test as regards biting (19:7%), attacking (7:3%), squealing (46:30%), mouth opening (1:0%), laying back ears (40:13%), puffing (7:0%), and urinating (42:27%), and also in number of reactions per individual (2.15 : 1.77). The blacks plus black hoodeds exceed the grays plus gray hoodeds in whining (23:6%), chittering (7:4%), defecating (63:40%), and no reaction (10:6%).

From this table compared with Table I, it will be seen that familiarity with the experimentor and experimental conditions in grays plus gray hoodeds has probably reduced biting (40% to 19%), attacking (9% to 7%), squealing (68% to 46%), laying back ears (45% to 40%), puffing (10% to 7%), whining (18% to 6%), chittering (18% to 4%), urinating (51% to 42%), defecating (70% to 40%), and has increased no reaction (1% to 6%). The average number of reactions per individual is decreased from 3.22 to 2.15.

The excitement of being the last rats taken from the cage apparently has increased for blacks and black hoodeds

the number of reactions from 1.27 to 1.77. It has increased defecating from 47% to 63%, urinating from 7% to 27%, chittering from 3% to 7%, whining from 10% to 23%, laying back ears from 10% to 13%. In spite of this evidence of greater excitement in the blacks, attacking remained the same as formerly (3%), squealing decreased from 37% to 30% and biting was reduced from 10% to 7%. It will be noted that whining and chittering probably increased at the expense of squealing.

When these figures are examined statistically the differences between the responses of grays and blacks have been reduced so that those for biting, attacking, squealing, whining, chittering, urinating and no reaction have lost significance. Defecating has questionable significance. Laying ears back is highly significant.

First Emergence Test

In the first emergence test, designed merely to determine whether blacks emerged from the nest more quickly than grays, the door of a cage was opened and the voluntary emerging order of rats with regard to their coat colors was recorded for all the rats emerging during five minutes. The results are given in Table III. It will be seen for example, that 14% of the albinos achieved the distinction of being first emergent, 13% of the grays, 9% of the gray hoodeds, 30% of blacks, but none of the black hoodeds. Grays and gray hoodeds together scored 12% first emergents, while blacks and black hoodeds scored 23% of first emergents. Grays and gray hoodeds together scored 27% of first, second, and third emergents, as against 53% for blacks plus black hoodeds. If we consider the total of all emergence, grays and gray hoodeds have 36% emergents compared with the record for blacks and black hoodeds of 60% emergents.

But upon the basis of behavior uninfluenced by cagemates, first emergence should be given greater weight than second emergence, second emergence greater than third, etc. This is because after the first three rats have emerged without calamity, even very cautious rats may follow suite. If we weight the actual numbers of emergents (1st, 2nd, and 3rd) with factors of 3, 2, and 1 respectively and then divide by population size as we have done in Table III, we get a score of .55 for gray and gray hoodeds to be compared with 1.27 for black and black hoodeds.

TABLE III. First Emergence Test.

Coat Color	n	1st Emergent in %	2nd Emergent in %	3rd Emergent in %	1st 2nd + 3rd Emergents in %	4th Emergent in %	5th Emergent in %	6th Emergent in %	Total All 6 Emergents in %
Albino	28	14	14	7	36	7	0	0	43
Gray	45	13	4	13	31	4	4	2	42
Gray Hood	22	9 → 12	4	4	18 → 27	4	0	0	23 → 36
		X			S				S
Black	23	30 → 23	22	4	56 → 53	0	9	0	65 → 60
Black Hood	7	0	43	0	43	0	0	0	43

Weighted Scores

	n	1st Emergent	2nd Emergent	3rd Emergent	Total Score
Gray + Gray Hood	67	(8x3) 24	(3x2) 6	(7x1) 7	67|37 .55
Black + Black Hood	30	(7x3) 21	(8x2) 16	(1x1) 1	30|38 1.27

When statistically examined, the difference in percentage for blacks and grays of individuals recorded as "first emergent" is not significant. But when first, second and third emergents are considered together, the difference between blacks and grays becomes significant. This difference is retained so that when all six emergents are considered together the diversity of response between gray and black is also significant.

Because this rough emergence survey indicated such distinct differences in behavior, it was decided to refine the test.

Refined Emergence Test

In the refined emergence test the door of each cage was opened in sequence and the time of emergence for each individual during three minutes was recorded by means of a stop watch. The results of the refined emergence test are recorded in Table IV.

It will be seen that of all animals emerging, grays and gray hoodeds averaged 84 seconds whereas the average time for blacks and black hoodeds to emerge was 57 seconds.

If the individual records are broken up into those emerging during the first, first-and-second, and first-second-and-third minutes respectively, 21% grays and gray hoodeds are found to have emerged during the first minute compared with 40% of the blacks and black hoodeds. During the first and second minutes, 40% of the grays and gray hoodeds emerged as compared with 63% of blacks and black hoodeds. During all three minutes a total of 49% of the grays and gray hoodeds emerged, whereas during this same time interval 73% of the blacks and black hoodeds emerged.

If one compares percentage of blacks emerging during the first minute with percentage of grays emerging during the first minute, the difference is not statistically significant. But if one compares blacks and grays emerging during both first and second minutes the difference is significant. When emergents of first, second and third minutes are compared, the behavior of blacks is significantly different from that of grays.

If one weights the emergents of the first minute with a factor of 3, emergents of the second minute with a factor of 2, and emergents of the third minute with a factor of 1, then the grays and gray hoodeds make a score of 1.10 to be compared with the black and black hoodeds score of 4.06.

Smoke-Blocked Emergence Test

Because it was noted that the gray rats were quickly becoming accustomed

TABLE IV. Refined Emergence Test.

Coat Color	N	Number Emerging		Total Seconds	Average Emergence Time in Seconds		% Emerging During 1st Minute		% Emerging During 2nd Minute	% Emerging During 1st + 2nd Minutes		% Emerging During 3rd Minute	% Emerging During 1st+2nd+3rd Minutes	
Albino	28	15		805	54		36		18	53		0	53	
Gray	45	21	33	1644	78	84	22	21	18	40	40	7	43	49
Gray Hood	22	12		1132	94		18		23	41		14	54	
Black	23	16	22	918	57	57	35	40	26	61	63	9	69	73
Black Hood	7	6		336	48		57		14	71		14	86	

Weighted Scores

	N	1st Emergent	2nd Emergent	3rd Emergent	Total Score
Gray + Gray Hood	67	(66×3) 42	(20×2) 20	(12×1) 12	67)74 1.10
Black + Black Hood	30	(23×3) 69	(20×2) 40	(3×1) 13	30)122 4.06

to the observer, it was decided to obliterate the human scent by the employment of tobacco smoke and repeat the emergence test.

Two puffs of strong cigar smoke were blown into each of the two compartments of the cage. Emergence was then timed for three minutes and recorded on the individual behavior records for each animal. Data have been recorded as previously, except that the population tested is smaller due to interim execution. The results are shown in Table V.

It will be noticed that the scores in Table V correspond rather closely to those of the emergence test made March 4, in spite of the smoke, although in Table V the effect of the smoke may possibly be evidenced by the lesser score of the grays (45:49%). The score of the blacks is several per cent higher in the March 26 test. When the scores for first, second and third emergence are weighted, there is less difference between gray and black, possibly due to grays making more places, and albinos doing better than previously with respect to the blacks. The test was made in the afternoon rather than in the morning. This fact may also have affected the score.

But in spite of all this, the blacks and black hoodeds still make better scores than grays and gray hoodeds and timed emergence is strongly in favor of the blacks as being the less timid. When blacks are compared with grays, the difference for emergents of the 1st minute is not significant. The difference for emergents of the first and second minutes combined is significant as is the difference for emergents of the first, second and third minutes combined.

Fourth Emergence Test

A fourth emergence test was made on April 2. The results shown in Table VI, are in accord with those of the previous tests. An innovation was added to this test. At the time the fourth emergence test was carried out it was noted that most of the rats were dozing. Thus, only the rats that happened to be awake would be recorded, which would bias the results. Hence the observer stirred up the rats in each cage with his gloved hand to awaken them and immediately started timing their emergence. The result was that an excitement factor was thus introduced.

It will be recalled that in the first emergence test the difference in percentage of blacks and grays recorded as "first emergent" was not significant. In the refined emergence test the difference

TABLE V. Smoke-Blocked Emergence Test.

Coat Color	n	Number Emerging		Total Seconds		Average Emerging Time in Seconds		% Emerging During 1st Minute		% Emerging During 2nd Minute	% Emerging During 1st + 2nd Minutes		% Emerging During 3rd Minute	% Emerging During 1st + 2nd + 3rd Minutes	
Albino	25	12		788		65.67		28.00		12.00	40.00		8.00	48.00	
Gray	40	18	27	1883	100.37	104.61		10.00	10.00	15.00	25.00	24.67	20.00	45.00	45.00
Gray Hood	20	9		827		91.89		10.00		20.00	30.00		15.00	45.00	
Black	24	18	22	1621	89.36	90.05		20.83	24.14	33.33	54.17	55.17	20.83	75.00	75.86
Black Hood	5	4		345		86.25		40.00		20.00	60.00		20.00	80.00	

Weighted Scores

	n	1st Emergent	2nd Emergent	3rd Emergent	Total Score
Gray + Gray Hood	60	(9×3) 27	(5×2) 10	(3×1) 8	60|45 0.78
Black + Black Hood	29	(7×3) 21	(7×2) 14	(5×1) 5	29|40 1.38

in percentage of blacks and grays emerging during the first minute was not significant. This was also true for the smoke-blocked emergence test. In contrast to these results it will be noted that the difference in percentage between grays and blacks emerging during the first minute in the fourth emergence test is highly significant. In none of the other emergence tests is the difference between blacks and grays emerging during the first and second minutes combined highly significant, but in the fourth emergence test this difference is highly significant. It seems probable that these differences between the results of the fourth emergence test when compared with the other three emergence tests, are due to the excitement factor introduced. This would appear to indicate that grays were more disturbed by the stirring than were blacks.

Annoyance Test

The annoyance test consisted of tickling the nose of each rat in its cage with fine brush bristles one inch long fastened to a long wire handle. Data were recorded for the behavior of the individual rats. When these data are summarized as shown in Table VII, it will be seen that grays and gray hoodeds vs. black and black hoodeds made reactions as follows: biting (86:20%), attacking (28:13%), squealing (21:10%), erecting hair (7:0%), snorting (3:0%), chittering (10:7%), hiding (1:0%), nibbling (0:3%). Fifteen per cent of grays and gray hoodeds made no reaction at all as compared with 73% for blacks and black hoodeds.

We may compare the reactions of individuals in the annoyance test with the reactions of the same individuals in the first holding test. If we seek out the records for those individuals that made no reaction to the holding test (H-test) and tabulate their reactions to the annoyance test (A-test) we find that 75% of these rats made no reaction to the annoyance test as well. They had a record of 16% biting, 8% attacking, and 8% nibbling. Under both tests these individuals were relatively undisturbed.

When the figures for the annoyance test are compared for differences in reactions between grays and blacks, biting and no reaction are found to be highly significant. Differences in chittering are of questionable significance.

If we select those individuals that made no reaction to the annoyance test

TABLE VI. Fourth Emergence Test.

Coat Color	n	Number Emerging	Total Seconds	Average Emerging Time in Seconds	% Emerging During 1st Minute	% Emerging During 2nd Minute	% Emerging During 1st + 2nd Minutes	% Emerging During 3rd Minute	% Emerging During 1st + 2nd + 3rd Minutes
Albino	25	8	612	76.50	12.00	16.00	28.00	4.00	32.00
Gray	39	18	1413	78.50	20.51	12.82	33.33	12.82	46.15
Gray Hood	20	10	628	62.80	20.00	30.00	50.00	0.00	50.00
Black	22	17	954	56.12	50.00	22.73	72.73	4.54	77.27
Black Hood	6	5	208	41.60	66.67	16.67	83.33	0.00	83.33

	n	1st Emergent	2nd Emergent	3rd Emergent	Total Score
Gray + Gray Hood	59	(8×3) 24	(9×2) 18	(4×1) 4	59 ÷ 46 0.78
Black + Black Hood	28	(10×3) 30	(4×2) 8	(5×1) 5	28 ÷ 43 1.54

regardless of color and tabulate their reactions to the first holding test, we find biting 19%, attacking 3%, squealing 72%, laying ears back 28%, snorting 3%, chittering 6%, urinating 31%. None of these animals defecated.

The records of these relatively undisturbed individuals in the holding test (as selected by their undisturbed reactions to the annoyance test) may be compared with the reactions of the individuals to the holding test selected on the basis of their having attacked and bitten in the annoyance test. The holding test records of animals that made no reaction to the annoyance test vs. the holding test records of animals that bit in the annoyance test give biting (19:59%), attacking (3:38%), squealing (72:69%), opening mouth (0:3%), laying ears back (28:55%), snorting (3:14%), chittering (6:7%), urinating (31:59%), defecating (0:69%), whining (0:31%), no reaction (28:3%). It will be seen that those animals chosen on the basis of disturbance in the annoyance test are much more disturbed in the holding test than are animals chosen on the basis of having made no reaction to the annoyance test.

If figures for the holding test of individuals that made no reaction to the annoyance test are compared with figures for the holding test of individuals that bit in the annoyance test, we find that differences in percentage of biting and of attacking are highly significant. Differences in laying ears back, urinating and no reaction are significant.

These comparisons indicate that the individuals most disturbed in the holding test are largely the same animals as are disturbed in the annoyance test, and that the animals undisturbed in the holding test are largely those undisturbed in the annoyance test.

Thus, we are dealing with individual similarities of reaction called forth by diverse situations indicating a constancy of behavior basis in the individual. Such a finding is commonly encountered by other investigators and was assumed in these studies.

TABLE VII. Annoyance Test.

Annoyance Test				Comparison of H vs. A Tests			
				All Colors			
Color of Segregates	Gray + Gray Hood	Black + Black Hood	Significance of Difference	H records when A is no reaction	A records when H is no reaction	H records the same as A	Significance of Difference
Number of Rats	67	30		32	12	29	
% Biting	06	20	hs	19	16	59	hs
% Attacking	28	13	x	3	8	38	hs
% Squealing	21	10	x	72	0	69	–
% Opening Mouth	0	0	–	0	0	3	–
% Erecting Hair	7	0	–	0	0	0	–
% Laying Ears Back	0	0	–	28	0	55	s
% Snorting	3	0	–	3	0	14	x
% Chittering	10	7	s?	6	0	7	x
% Nibbling	0	3	–	0	8	0	–
% Hiding	1	0	–	0	0	0	–
% Urinating	*	*	–	31	*	59	s
% Defecating	*	*	–	0	*	69	–
% Whining	0	0	–	0	0	31	–
% No Reaction	15	73	hs	28	75	3	s

*Could not be determined.

Garlic Test

It had been noted previously that no rat of this series liked the smell of an onion and it was believed from untimed observations that albinos were less sensitive, or at least made less response to having a piece of onion held before the nose, than did rats of other coat colors.

Hence it was decided to time the repulsion reactions of individual rats to a piece of garlic (*Allium sativum*). The test piece was fastened to the end of a long wire and approached to within about 2 mm. of the rat's nose. Timing was with a stopwatch.

Mrs. Wilkinson (caretaker) reported that Wistar albinos, as compared with other rats in the laboratory hesitate a long time, rather bewildered "as though they didn't know what it was all about" when one offers them a piece of food. She stated that other rats sniff for an instant and either take the food if they like it, or if they don't like it, they back away from it. Both Miss Meeser (Asst. Curator of the Colony) and Mrs. Wilkinson aver that when rats have tasted

something they do not like, they may push the floor away in front of them with both paws, or they may run along rubbing their mouths on the floor.

If one examines the results of this garlic test, shown in Table VIII, one finds that 71.43% of albinos backed away after sniffing the garlic for an average of 9.87 seconds, as compared with 50.91% of grays and gray hoodeds that backed away after an average of 4.28 seconds, and also as compared with blacks and black hoodeds 89.28% of which backed away from the garlic after an average of 5.48 seconds. The smelling and then backing away appears to be a definite olfactory test, the animal backing away because he does not like the odor of allyl sulphide $(C_3H_5)_2S$.

When the difference in percentage of grays that sniffed the garlic and backed away are compared with the percentage of blacks making the same reaction, the difference is found to be highly significant.

4.76% albinos, 18.92% grays, 22.22% gray hoodeds, 0% blacks, and 28.57% black hoodeds attacked the onion in average times as follows: 1.00 secs., 2.00 secs., 2.25 secs., 0.00 secs., and 1 sec. The reactions of these animals are less understandable. Did they quickly smell the garlic, and attack it because they hated the odor, or did they attack because they saw a strange object quickly appear before their faces, not having received or interpreted the odor at all? Indeed, there may be mixed motives represented in this protocol.

The difference in behavior between blacks and grays here is not significant.

23.81% albinos, 16.23% grays, 11.11% gray hoodeds, 4.76% blacks and 0.00% black hoodeds bit the garlic after sniffing for the following average times: 3.60 secs., 4.67 secs., 5.00 secs., 4.00 secs., and 0.00 secs. respectively. This reaction appears to consist of careful olfactory testing followed by the desire to test the taste of the garlic as possible food. However, this group may possibly contain animals that finally became angry enough to bite the garlic although not exhibiting actual attack. The differ-

TABLE VIII. Garlic Test.

Coat Color	n	% Backed away after. Av. time in seconds		% Attacked after. Av. time in seconds		% Bit garlic after. Av. time in seconds		Miscellaneous reactions after. Time in seconds
Albino	21	(n=15) 71.43% 9.87 secs.		(n=1) 4.76% 1.00 secs.		(n=5) 23.81% 3.60 secs.		
Gray	37	(n=21) 56.76% 4.09 secs.	(n=28) 50.91%	(n=7) 18.92% 2.00 secs.	(n=11) 20.00%	(n=6) 16.23% 4.67 secs.	(n=8) 14.54%	1. Jumped back 4. Fled 1. Grabbed garlic
Gray Hood	18	(n=7) 38.89% 4.86 secs.	4.28 secs.	(n=4) 22.22% 2.25 secs.	2.09 secs.	(n=2) 11.11% 5.00 secs.	5.75 secs.	3. Rubbed nose 1. Ran 1. Grabbed garlic 3. Opened mouth 3. Opened mouth
Black	21	(n=20) 95.23% 6.15 secs.	n=25 89.28%	(n=0) 0% 0.00 secs.	(n=2) 7.14%	(n=1) 4.76% 4.00 secs.	3.57%	
Black Hood	7	(n=5) 71.43% 2.80 secs.	5.48 secs.	(n=2) 28.57% 1.00 secs.	1.00 sec.	(n=0) 0.00% 0.00 secs.	4.00 secs.	
Significance of Gray vs. Black difference in percentage		hs		x		x		

ence in time between this reaction and the attack make them appear distinct as is shown in Table VIII. However, examination of the figures reveals the fact that there is no significance in the difference between the reactions of blacks and grays.

Curiously enough, the grays and gray hoodeds are still indicated as wilder rats than the blacks and black hoodeds by the following analysis: although 50.91% of grays backed away from the garlic as compared with 89.28% of the blacks, still it took the blacks an average of 1.20 seconds longer before they reacted. Furthermore, 20.00% of grays and gray hoodeds attacked the garlic as compared with 7.14% of blacks and black hoodeds. If the miscellaneous reactions are credited, the grays and gray hoodeds are found to be still much more wild than indicated by these figures.

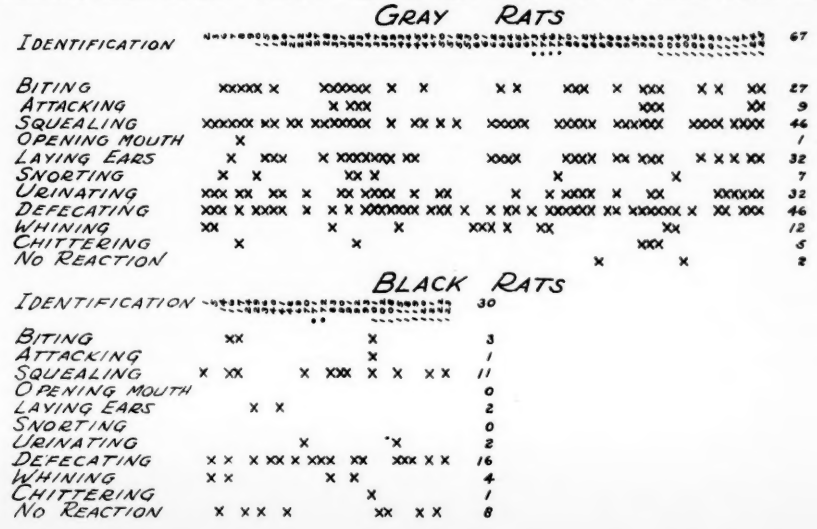
But a quite unexpected result is also derived from this test: 71.43% of albinos require 9.87 secs. before backing away from the garlic. Combined grays and blacks give 66.26% backing away after 4.85 secs. This would seem to indicate very definitely that the albino rat is much less responsive than the pigmented animals.

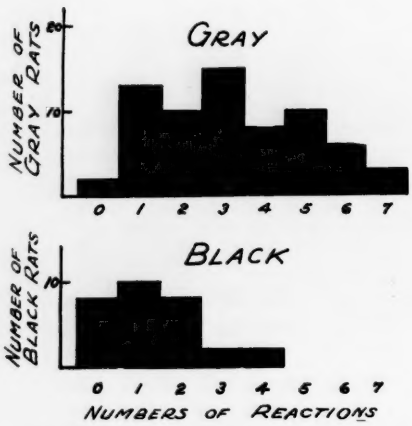
To check this observation on other animals, the garlic was held before 10 Hatai black hoodeds that backed away from it after an average of 7 seconds, whereas a corresponding number of Wistar albinos never did back away from it, but after a time, (about 15 secs.) three of them tested it with their teeth. So far as coat-color genes are concerned (Wistar albinos are Hatai hoodeds plus albinism), it would appear that extreme dullness of the olfactory sense is brought about by the albino gene.

Discussion

The foregoing data have given clear indications that marked differences in behavior exist between gray and black segregates, but the tests do not separate animals of the two coat colors sharply. With any "trait" as fluid and pervasive as temperament, even if differentiated by a single gene substitution, we would not expect any such division. Wild animals are distinguished from tame animals not by a single reaction, but by a cluster of reactions, by a tendency to react more violently with excitement. Many cases have been reported in the literature wherein the presence of a gene is unmistakable but with its expression varia-

TABLE IX. Data of the First Holding Test. Small numbers identify individual rats. A dot beside the identification number indicates a backcross animal. All others are F_2 animals. × indicates reaction made.

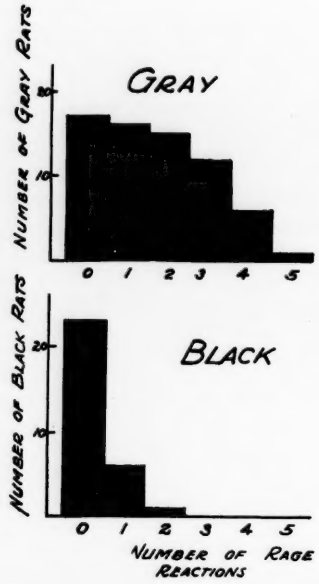




TOTAL REACTIONS COMPARED

Figure 2

Histograms for comparing the numbers of reactions per individual among gray and black hybrid rats in the holding test.



RAGE REACTIONS PER INDIVIDUAL

Figure 3

Histograms for comparing the number of rage reactions per individual among gray and black hybrid rats in the holding test.

ble — sometimes over a considerable range.

In this experiment, the grays contain individuals some of which carry the black gene in one dose, and others of which do not carry the black gene at all. The blacks on the other hand, are all homozygous for the black gene, because black is a mendelian recessive, and hence the black population is genetically more uniform. Thus, if behavior trends are correlated with coat-color genes, the blacks should show a more homogeneous group of behavior reactions, all having very low wildness scores unless influenced by association with wild litter mates.

In the wild individuals there is greater chance of showing taming effects due to a peaceful laboratory environment, than there is of individuals tame by nature becoming wild. And because the naturally wild individuals are largely grays, this environmental influence should also tend to make greater variability among grays.

The raw data of the first holding test have been arrayed in Table IX. If the various numbers of reactions made by different rats (regardless of type of reaction) are plotted against the number of individuals making each consecutive number of reactions, we find a relatively wider distribution (from 0 to 7 reactions) for grays and a more restricted distribution (from 0 to 4) for blacks. These facts are shown graphically in Figure 2.

When these data are examined statistically* it is found that for the gray distribution the mean is 3.2 with standard error of 0.2. The standard deviation is 1.8. $\beta_1 = .07$. $\beta_2 = 2.12$.

The value of β_1 for this sample at the

*Symbols used in these comparisons are as follows:
β_1 (beta$_1$) is a measure of skewness of the distribution function. (Pearson)
β_2 (beta$_2$) is a measure of kurtosis (flatness or peakedness). (Pearson)
s is the standard deviation of the sample. (Fisher)
σ (sigma) is the standard deviation of the theoretical distribution.
t is "Student's" distribution as modified by Fisher, used for the purpose of testing the critical value of differences between means.

two per cent point is .424 so that we would expect a normal curve to agree with the distribution. (See Pearson,[3] vol. II, p. 224).

A normal curve fitted to these data gives a value of chi-square of 4.87 and entering the table with 4 degrees of freedom (leaving 6 less mean plus standard deviation or 4 degrees). Since the end values were combined to increase the frequencies to at least nine, P = 0.30, which is satisfactory, according to Fisher, because it lies between 0.9 and 0.1.

The blacks have a mean of 1.3 ± 0.2. The standard deviation is 1.1. $\beta_1 = 0.47$. $\beta_2 = 2.88$.

In this case the values are such that a normal curve would fit the population. However, it was not satisfactory to fit a normal curve to the data owing to lack of number of divisions.

When we compare the mean for grays with the mean for blacks we find, using Fisher's terminology, s = 0.1474, t = 42.6180, P < .001. Hence the difference is highly significant. This curve fitting has been carried out to see if the data represent a normal distribution, in which event the tests for significance are more accurate than if they do not represent a normal distribution.

By inspection of the original data it will be seen that such reactions as squealing, whining and defecating are very commonly found in both grays and blacks and hence may not be good indications of temperamental differences. In fact, they may actually be extraneous to the general group of reactions associated with what may be called rage. Chittering and opening the mouth are too rare to be of much value.

If we plot the remaining data (i.e., those for biting, attacking, laying ears back, snorting, urinating) in order to isolate for comparison the rage cluster of reactions, we find the facts depicted in Figure 3. Both the gray and black curves are moded at 0. Blacks fall off sharply, there being but one rat making as many as two rage reactions. On the contrary, the gray curve continues high, there being 16 rats making one rage reaction, 15 rats making two rage reactions, 12 rats making three rage reactions, 6 rats making four rage reactions, and 1 rat making five rage reactions. Thus, by removing those reactions not supposed to be associated with rage, the differences between grays and blacks are more accentuated than when we considered all reactions regardless of type.

When we study the distribution of these reactions for grays we find mean = 1.6 ± 0.1. Standard deviation = 1.3. $\beta_1 = 0.14$. $\beta_2 = 2.16$. The theoretical population has probably a Pearson Type I curve.

The black distribution has a mean of 0.3 ± 0.1. The standard deviation is 0.5. $\beta_1 = 3.14$. $\beta_2 = 5.20$. The theoretical population probably has a Pearson Type I curve. (See chart on p. 66, Pearson,[3] vol. I).

The means for grays and blacks may be compared. Here it is found that s = 0.2147, t = 40.3964, P < .001. Hence, the difference between the means is highly significant.

Another difference observed between gray and black rats is the intensity of reactions made. The squeal of the gray rat is frequently loud and prolonged; that of the black, a short cry of no great intensity which may degenerate into a protesting whine. Urinating frequently consists of a strong spurt or stream in the gray as compared with the slow emission of one or several drops in the black. Defecation frequently includes the extrusion of three to five boluses in grays, but more often of a single bolus in blacks. Biting in the gray rat may entail a series of six or seven forceful bites delivered with machine-gun rapidity; in the black it is often a single, weak nip.

Summary

1. Two holding tests, four emergence tests, and an annoyance text give similar results indicating the greater wildness and savageness of animals bearing a gray coat compared with those having a black coat in a population of 125 segregates of crosses of tame albino (carrying black) with wild gray Norway. It is likely that

pleiotropy accounts for this association between coat color and temperament.

2. Comparison of the annoyance test with a holding test shows the most annoyed and the most undisturbed rats in each test to be largely the same individuals, as would be expected, if the basis of wildness and savageness remains relatively constant in the individual under different situations.

3. A garlic test suggests differences between gray and black segregates in the sense of smell. It also suggests that the albino gene has a profound dulling effect upon that sense.

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The British Birth Rate

The serious threat to our population due to the falling birth rate continues to attract attention. Prof. Munro Kerr, president of the Obstetrical and Gynecological Section of the Royal Society of Medicine, has made a medical contribution to the discussion in the form of a communication to the *Times*. The annual birth rate per thousand of population for England and Wales was 32.4 for the decade 1881-1890 (average), 18.3 for the decade 1921-1930 (average), 14.9 for the year 1939 and 14.6 for the year 1940. Up to the present the fall in the birth rate has been offset to a considerable extent by the dramatic fall in the infant death rate in the present century—from 150 to 55 per thousand live births. But this compensation must necessarily diminish. Notwithstanding the general fall of infant mortality there has been little lowering of the stillbirth rate or neonatal (first month) mortality, as these figures show:

Rates per Thousand Live and Stillbirths (England and Wales)

Year	Stillbirths	Neonatal Death Rate (Ages 0-4 Weeks)	Combined Rate
1928	40.1	29.8	69.9
1929	40.0	31.5	71.5
1936	39.7	29.0	68.7
1937	39.0	28.6	67.6

Munro Kerr states that not all these deaths are preventable, but something between 30 and 50 per cent could be prevented by improved antepartum, intrapartum and postnatal care. For this purpose he has been advocating for twenty years a national maternity service in which obstetric specialists and the public health service would work in cooperation. He quotes from the brochure Population and Fertility, issued by the Population Investigation Committee in 1939 under the editorship of D. V. Glass (statistician) and C. P. Blacker (physician and secretary of the Eugenics Society): "The causes of the decline of fertility are numerous, complex and deep seated. In western European countries they form so intimate a part of the twentieth century view of life that effective countermeasures will not be easy to find. What we should do is not to suppress birth control but to remove as many as possible of the obstacles impeding the free expression of the parental instinct. Conditions should be created in which people would want to have children."

Munro Kerr thinks that there is little prospect that the birth rate can be increased unless the government tackles the problem seriously and introduces radical measures. Unfortunately no political party looks far ahead or has much vision. That is left to small minorities who are called "alarmists." He warns the government, as others have done, that the situation will become desperate in some years, when hurried legislation will be too late.—*J. A. M. Assoc.* July 4, 1942.

POLYDACTYLY, A SUB-LETHAL CHARACTER IN THE PIGEON

W. F. HOLLANDER AND W. M. LEVI
Palmetto Pigeon Plant, Sumter, S. C.

A PIGEON with double hind toes was illustrated in this JOURNAL for 1916 (p. 321). The bird was a domestic pigeon (Racing Homer) found in Australia, and it lived to maturity. Mated with a sister, it produced an offspring which had an extra toe on one foot. According to Fontaine[2], extra toes are found in the Syrian variety of the Spot breed (*le pigeon huerté syrien*), but he gives no further details or illustrations. This variety has apparently never been described elsewhere, and its existence seems questionable.

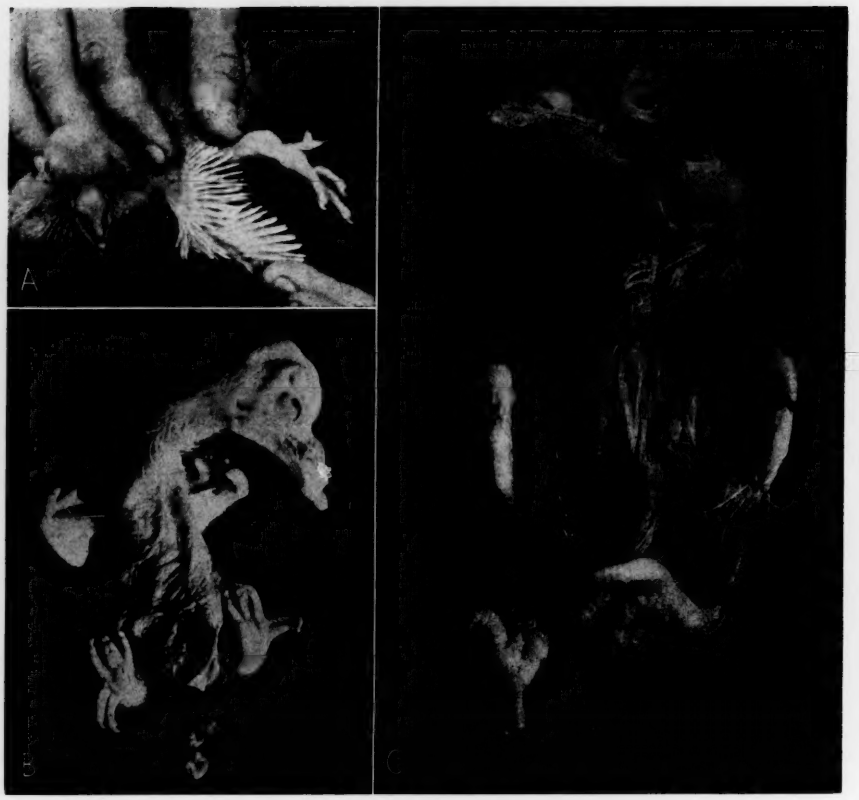
The above references are the only ones, to our knowledge, up to 1941 on the occurrence of polydactyly in pigeons.

In August, 1939, a polydactyl squab appeared at the Palmetto Pigeon Plant oi Sumter, S. C. The parents were Silver King pigeons, both perfectly normal (mating K17-531). Each of the squab's feet had an extra hind toe, just as shown in the 1916 illustration; in addition, each wing had an extra thumb (see Figures 5*A* and 4*A*). A photograph of this squab at the age of about five days is given by Levi[3] (p. 240).

This squab was given careful attention. It was very plump and fat, but was retarded in growth and had a chronic wheeze or rattle in breathing. At weaning age (about one month) it was removed from the adult pigeons and placed in an individual coop. It showed no ability to feed itself and had to be hand-fed. At this time it was considerably smaller than normal Silver Kings of the same age, and was abnormal in several other respects. The lower beak projected nearly an eighth of an inch beyond the upper; the legs were short, particularly the tarsi, giving a squatty, duck-like appearance; and the plumage was somewhat defective. The main tail and wing feathers were somewhat frayed and twisted, and there were only six rectrices instead of the normal twelve. The bird could not fly, and had some difficulty even in walking. In spite of good care and superficial healthiness—no emaciation—it died at the age of 35 days. Autopsy failed to reveal the cause of death; the internal organs appeared normal. The sex was female.

In the following year (1940) more polydactyl squabs appeared, not only from the same parents but from three other pairs of Silver Kings (matings K17-534, K15-453, and K7-365). Two more pairs of Silver Kings produced polydactyls in 1941 (K15-457 and K3-422). From these six pairs a total of 24 polydactyl squabs has been obtained. An additional specimen of unknown parentage was found under foster parents in 1940; its color indicated that it, too, was of Silver King origin. None of the polydactyls lived to maturity in spite of better than ordinary care. Though often placed under the best foster-parents, the majority died at less than three weeks of age from no definite ailment.

Although these polydactyls all resembled each other to some extent, there was nevertheless a wide variation. An exhaustive study of the anatomical differences has not been attempted, but a brief survey of the range is desirable. Of the 25 specimens, 18 were preserved for study, and these are probably a fair sample. The feet varied from having only a single, broad, flat hind toe with two claws to fantastic hand-like extremities with six digits and up to seven claws. Leg length varied from slightly below normal to very much shorter. Extra thumbs on the wings were absent in several cases. At the other extreme, two young which died before hatching



POLYDACTYL SQUABS

Figure 4

A—the first polydactyl discovered at an age of about one week. Note the extra hind toe, the extra thumb on the wing, and the undershot beak. The bird is a female and is classified as Group II. *B*—An extreme (Group IV) polydactyl female which failed to hatch. Note the multiple thumbs on the wings and their paw-like appearance. On the feet the extra toes are markedly distorted. The undershot beak and the short down are also characteristic. *C*—The female polydactyl from the White family,—not closely related to the others shown here. The extra toe and the undershot beak resemble the Silver King polydactyl, but the wings and the down are normal.

had wings so extremely polydactylous that they resembled embryonic mammalian fore-paws. All the polydactyls except one had undershot beaks; and that one, which lived to 45 days, had upper and lower beaks of equal length, without the normal tendency for the upper to hook over the lower. The tail feathers were of sufficient length to be counted accurately in only six cases. Only one bird in addition to the first had a subnormal number; two others were normal, and the remaining two had one more than normal. The plumage was slow-growing in all specimens, and somewhat defective in the two older specimens which had fully developed feathers (see Figure 7). Another peculiarity observed in all cases which were examined early enough was shortness of the nestling down, similar to the condition found in young of "dilute"

POLYDACTYL FOOT AND "HAND"

Figure 5

At left, the "hand" region of the right wing of a Group III polydactyl male, which survived 15 days. Some feathers have been removed to show the extra thumb (indicated by arrow). At right, is the right foot of a Group II polydactyl dead at 35 days.

coloration. Normal Silver Kings are not of this type (Levi,[3] p. 222).

Correlated Variation

All the above abnormalities were clearly correlated in their variation. That is, the more abnormal a squab was in regard to one feature, the more abnormal it tended to be in regard to the others. This correlation was not perfect, but it should be noted that a small degree of asymmetry or difference between right and left sides in regard to any one feature was found in many of the specimens (Figure 6). Because of the correlation it was rather easy to classify the polydactyls into four grades or groups, as follows:

Group I. No extra thumb or only on one wing; single extra hind toe, generally more or less joined with other toe.

Group II. Single extra thumb on both wings; single extra hind toe on each foot, usually not joined with other toes.

Group III. Single, usually large, extra thumb on each wing; two extra toes or claws on one or both of the feet.

Group IV. More than one extra thumb on each wing; two or more extra toes or claws on one or both feet; feet distorted.

Only one specimen, a 24-day-old male, did not fit into this grouping. This squab had two extra toes or claws on each foot, but an extra thumb on only one wing. It seemed to be a compromise between groups III and I, and hence was placed in group II. The frequencies in the four groups are roughly equal except for group IV, which has only two representatives.

When the ages at death in the different groups are compared (see Figure 9), it is seen that there is a definite correlation between the grouping and life expectancy. The more abnormal a squab is, the poorer are its chances to live to a given age. Sex, however, appears to have little or nothing to do with the grouping or with age at death, although the three oldest specimens were all females. As the female in pigeons is the heterogametic sex, and generally the weaker under adverse conditions, it is

MULTIPLE TOES

Figure 6

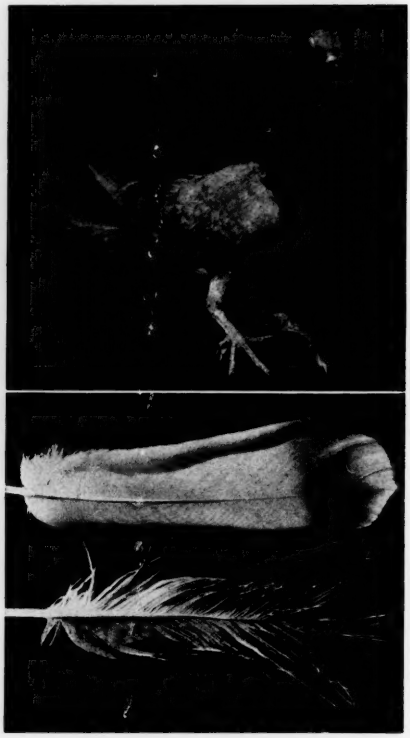
Feet of a Group III polydactyl dead at 20 days. Note the joined extra hind toes on the right foot and the broad extra toe with two fused claws on the left foot. Note also the short thick tarsi.

interesting that the female polydactyls were at least equal to the males in vigor.

Inheritance

The stock of Silver Kings here involved originated from a few pairs of 1935-bred birds obtained from the pigeon farm of G. W. Middleton and Sons, in Norristown, Pa. In answer to an inquiry about the polydactyls, they stated that they "occasionally get a squab like this" (pers. com., 1940). Evidently then this stock can be expected to produce the condition regardless of environment. However, it must be noted that not one of the very numerous offspring of the original pairs was polydactyl, nor were any of the far more numerous second generation descendants of that type. Polydactyls appeared only in the third and fourth generations.

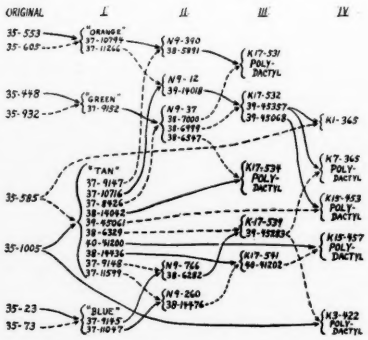
An investigation of the pedigrees reveals two very significant facts. In the first place, no inbreeding occurred before the production of the third generation (because it has been a breeding policy here to discourage brother × sister matings). In the second place, all the polydactyls trace back on both maternal and paternal sides to one of the original pairs—the parents of the "Tan" family. In other words, the polydactyls were produced by inbreeding, from matings of birds related to each other only through that particular pair of original Silver Kings. These facts all suggested the following explanation: that the polydactyls are homozygous for a simple Mendelian



POLYDACTYL METHUSELAH

Figure 7

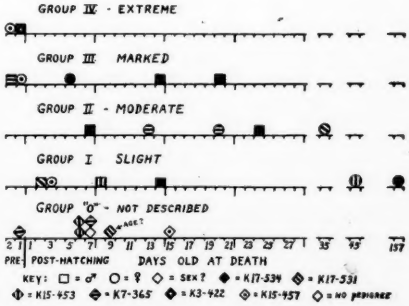
This female lived to the age of 157 days, which far exceeded the life-span of any other extra-toe bird. She was classified as a squab in Group I, the least abnormal type. Below is shown a tail-feather from this bird compared with a normal tail feather, to show the defective structure.



RELATIONSHIP OF POLYDACTYLS

Figure 8

Pedigree chart of the Silver King polydactyls. The generations progress from left to right. The male line is drawn solid and the female dotted. Sibs are enclosed in a bracket and headed by the mating number or name of the parents.


GROUP IV - EXTREME
GROUP III MARKED
GROUP II - MODERATE
GROUP I SLIGHT
GROUP "0" - NOT DESCRIBED
AGE?
2 1 3 5 7 9 11 13 15 17 19 21 23 25 27 35 49 157
PRE- POST-HATCHING DAYS OLD AT DEATH
KEY: □ = ♂ ○ = ♀ ◇ = SEX? ◆ = K17-534 ◈ = K17-531
◈ = K15-953 ◈ = K7-365 ◆ = K3-922 ◈ = K15-957 ◇ = NO PEDIGREE

VITAL STATISTICS OF POLYDACTYLS

Figure 9

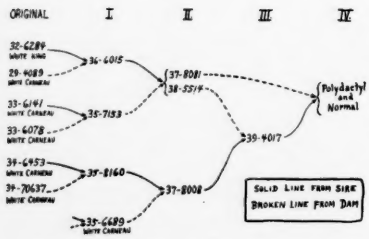
A tabulation to show the relationships between the degree of polydactyly (group classification), sex, family, and age at death.

recessive factor, which was introduced by one of the parents of the "Tan" family. To test these original birds, each was mated with a descendant which had produced polydactyls. The new mating involving the old male (K3-422) supported the theory by producing a polydactyl, and the new mating involving the old female (K1-365) also supported it by not producing any. It appears therefore that the original male, 35-1005, was the sole source of the trait. (See pedigree chart of the polydactyls—Figure 8).

The theory that polydactyly is a simple Mendelian recessive in inheritance is further supported by the ratio of 91 normal to 24 polydactyls produced by the six matings (Table I). This ratio is not significantly different from 3:1 (expectation 86:29).

A final test was made to ascertain whether polydactyly could be produced without inbreeding—whether some chromosome aberration, rather than a recessive factor, might be responsible. Matings K17-534 and K15-453, which had produced polydactyls, were broken up. The male parents were mated with ordinary females of the White Carneau breed (matings K11-330 and K11-349), and the female Silver King parents were mated with White Carneau males (matings K12-353 and K12-359). These four new matings produced a total of 42 squabs from 43 eggs, and all young were normal. Adding mating K1-365, we have five matings of polydactyl-producers to pure normal pigeons. These laid a total of 54 eggs and raised 50 young, all normal. With such a low proportion of losses, there is certainly no indication of chromosome aberration here. Accordingly it appears unquestionable that the polydactyly and associated abnormalities are the effect of a simple Mendelian recessive factor, not sex-linked. We have given it the factor symbol *py*.

Since not one of the 25 polydactyls survived to maturity, in spite of our efforts to maintain them, we consider the *py* factor sub-lethal. The immediate cause of death has not been found, and most of the specimens seemed to be thriving the day before death. The respiratory trouble noted in the first polydactyl was also present in most of the others which lived to the second week or beyond, and might have caused death by suffocation, but ordinarily this ailment is not serious, and none of the specimens showed internal lesions severe enough to be fatal. The polydactyls in group IV (extreme) were so abnormal that they were unable to hatch. The fe-



WHITE POLYDACTYL PEDIGREE
Figure 10

This shows some remote relationship to the Silver King breed wherein the other polydactyls appeared.

male which lived to the age of 157 days would have died much younger under ordinary conditions, for the undershot beak made it difficult for the bird to pick up grain. It had to be hand-fed for some time after weaning, and would have starved to death later if feed and water had not been placed in the most obvious positions. Its eyes appeared to be normal but they did not focus forward properly, and the mental development seemed poor. The bird could not fly, and walked awkwardly. In short, whether extreme or slight, the expression of this factor makes for early death.

A Separate Occurrence of Polydactyly

By a remarkable coincidence polydactyly has also been discovered in an entirely unrelated family of pigeons at the Palmetto Pigeon Plant. This is a family of "Show White Carneaux," but not purebred, as a White King male figures in the immediate ancestry. The first polydactyl from this family appeared in 1940. The bird seemed fairly vigorous but died at the age of one day. There was a distinct extra hind toe on each foot, and the lower beak was somewhat undershot, but there were no extra thumbs on the wings and the nestling down was normal. The legs and tarsi seemed normally proportioned, not shortened (Figure 4*C*). This specimen was female.

The second polydactyl from this family failed to hatch. It closely resembled the first except that the extra toe on the left foot had two claws, and the sex was male. The parent pair produced in all 18 eggs, of which four were broken or lost, three had dead young embryos, and eleven produced describable squabs. Except for the two polydactyls, all young were quite normal.

An examination of the pedigree (Figure 10) shows that inbreeding is again involved. As purebred Carneaux have never been known to produce polydactyly, it is logical to place most suspicion on the King ancestor as the source of the trait, but in this case the original bird was dead and could not be tested.

To test whether the same factor was involved here as with the Silver Kings, this white pair and mating K17-531 were broken up and the mates interchanged. The White male with the female Silver King produced 22 eggs, from which 16 young were examined, all normal. Three of the remaining eggs were infertile and three had embryos dead at an early stage. The White female with the Silver King male produced 19 eggs, from which 13 young were described, all normal; one of the remaining eggs was lost, another infertile, three had young dead embryos.

TABLE 1. Matings of polydactyl-producers with each other (above), and with non-polydactyl-producers (below).

MATING	EGGS				SQUABS		
	NUMBER LAID	INFERTILE	DEAD YOUNG EMBRYO	LOST OR BROKEN	NORMAL	POLY-DACTYL	NO RECORD
K17-531	30		4	3	26	3	1
K17-534	40		1		22	7	4
K15-453	18				13	4	
K7-365	16	2	1		8	5	
K15-457	12				8	4	
K3-422	16		1		14	1	
TOTAL	132	2	7	3	91	24	5
K1-365	11			3	8		
K11-330	12				12		
K11-349	11			1	10		
K12-353	10				10		
K12-359	10				10		
TOTAL	54	0	0	4	50	0	0

and one produced a squab which was not examined. Although the number of dead embryos from these matings is rather high, it is no higher than in the original white mating, and it probably has nothing to do with polydactyly. If we judge from the young described, it appears unlikely that the two types of polydactyly are produced by the same factor, or even by different alleles. In any case it appears that the second type is similar to the first in being simple recessive, autosomal, and sub-lethal.

Discussion

At present only speculation is possible as to the causes of the wide variation of expression of the *py* factor. Modifying factors could be postulated, but the existence of some asymmetry suggests that the factor may be sensitive to slight differences in environmental conditions during incubation. Two types of polydactyly are now known in the chicken, and both of these are considerably variable also. Sturkie[5] has studied the effect of temporary chilling of young polydactyl embryos; this treatment appears to inhibit the development of extra toes in many cases. Perhaps variation in incubation temperature or other conditions has influenced the course of growth in the pigeons also; but it is interesting that no correlation of the grouping with season of the year could be found.

The two types of polydactyly in the chicken are not recessive as in the pigeon, but dominant to normal, and apparently allelic to one another. Further, their effects seem limited to the feet and wings, and viability is normal except in extreme variants.[6] The more common type of polydactyly in the chicken shows no extra thumbs on the adult wings, though the embryos are said to have them temporarily.[4] It is curious that polydactyly in the pigeon, while superficially similar to that in the chicken, should be so fundamentally different. It is possible that the cases reported from Australia[1] are a dominant type as in the fowl, as well as not being sub-lethal.

Our first impression of the pigeon polydactyls was that they suggested some grotesque prehistoric creature come to life. Probably they have little evolutionary significance, but they are of interest to the student of teratology. Dr. Walter Landauer has suggested (pers. com., 1940) that the condition may be analogous to the Laurence-Moon-Biedl syndrome found in certain human families. This syndrome is characterized not only by polydactyly and syndactyly but also by such features as obesity, hypogenitalism, and mental retardation.

Summary

A variable syndrome including polydactyly of feet and wings, shortened legs, undershot beak, short nestling down, and defective plumage was found in a family of Silver King pigeons. Of 25 specimens, none survived to maturity. Breeding data show that a simple recessive pleiotropic factor is responsible, which is symbolized *py*. A somewhat similar condition was also found in an unrelated family, and appears to be similar in inheritance but not allelic with the previous type.

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Population Growth in India

Preliminary returns of the Census of India of March 1, 1941, indicate a population of 388.8 millions, an increase of 50.7 millions since 1931. This increase of fifteen per cent is the largest in Indian census history, both relatively and absolutely. India now has a population which is not much smaller than that of all Europe outside of Russia. In the past decade its population increase alone amounted to more than the total population of the British Isles. The trend of growth of the Indian population has been almost cyclical.

The decade 1881 to 1891 was one of relative prosperity and yielded a recorded increase of 10.9 per cent. Because of the great famines in 1889 and 1900 the increase in the decades 1891 to 1901 was only 1.5 per cent. The decade of 1901 to 1911 was one of general recovery and brought a population increase of 6.5 per cent. Then followed, in 1911 to 1921, a negligible increase of 1.2 per cent owing to the death of at least thirteen million people from the influenza pandemic and to the generally higher mortality of the War and immediate post-War period. In the years 1921 to 1931 the rate of increase again went up, this time to 10.6 per cent. If the previous pattern of alternately large and small increases had continued, the decade 1931 to 1941 would have been one of small increase incident to famine, plague, or other catastrophes. However, in spite of the world depression, growth was more rapid than ever before, amounting to 15.2 per cent in the British Provinces and 14.3 in the Native States and Agencies.

The largest rates of increase occurred at the extreme points of the country, just as they have tended to do in the past. In the north, the Northwest Frontier Province, the Punjab, and the Punjab States Agency all increased by more than twenty per cent. Travancore, in the extreme South, grew by nineteen per cent, while in the extreme northwest, Bengal and Assam grew by twenty and eighteen per cent, respectively. Increases above the average appeared generally in the western section from Rajputana and Sind southward through the Bombay Presidency. Population decreases appeared only in the Baluchistan States. Delhi, Indian capital and a Chief Commissioner's province, increased by 44.1 per cent. The rate of increase in cities of over 100,000 was reported to be much higher than for all India, and the number of such cities increased appreciably. Individual rates of increase ranged from slightly less than eleven per cent to almost 100 per cent for the City of Cawnpore. No detailed statistics on urban growth were included in the census release. . . . *Population Index*, July, 1942.

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Horrible Example

THIS book details how Arizona and Montana gold and copper complicate the problem of heredity and environment in human development.* The chap who discovered these metals was the late "Copper King Senator," Clark of Montana. What fantastic quantities of copper did to the Senator, to his children and to the politics of the State whose natural resources furnished the Clark "pile," is harrowing and not altogether edifying reading. The ramifications of the Clark millions were fantastic, and they seem to have turned to ashes most of the people and institutions they happened to touch. If Mr. Mangum's picture of W. A. Clark, Jr., is accurate, even Phi Beta Kappa did not escape the Midas blight. Depending on how one looks at it, the book could furnish horrible examples both for the hereditarian and the environmentalist. It is too bad that Senator Clark was not identical twins, one of whom went West to seek his fortune, while the other continued to "plow straight and deep furrows" in Pennsylvania. Like so many of the "examples" of social plusses and minuses, this one doubtless proves lots of things up to the hilt, but in the light of present ignorance as to human ontogeny, it would be hard to tell what. Mr. Mangum documents the fact that the Clarks would hardly have been worse off if the Bannacks had put the head of the some-day Senator on a pole on page 19, instead of the head of one of their Blackfoot neighbors. And one gets the impression that Clark would have coldbloodedly considered even that "an interesting exhibition."

Surely one thing that it does prove is that a society wherein all of the "social advantages" of limitless wealth manage to furnish about as nightmarish an environment as the mind of man can conceive of, is not a society which has yet come to an effective adulthood. Perhaps, standing on the brink of leading the world to the New Jerusalem after World War II, this is a thought which might be sobering to some of our more enthusiastic global planners.—R. C.

*Mangum, Wm D. *The Clarks, An American Phenomenon.* With an introduction by Edward Alsworth Ross. Pp. ix-257. Illustrated. $2.50. Silver Bow Press, 289 Fourth Avenue, New York. 1941.

THE EFFICIENCY OF THREE METHODS OF SELECTION*

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Iowa State College

THE practical value of a plant or animal is almost always affected by several traits. Hence deciding which are the most valuable individuals to select for parents of the next generation forces the breeder to consider several different characteristics. These are not likely all to be equally important or all to be independent of each other. There are many ways of selecting for several different things but these will not often be equally efficient. The most efficient method is that which results in the maximum genetic improvement per unit of time and effort expended.

In planning some of their experimental work, the authors had occasion to compare the theoretical consequences of three fairly simple ways of selecting for net merit, considered as a compound of several different characteristics. While the results are not completely generalized, they are striking enough and seem to be of enough general validity to deserve presenting to plant and animal breeders.

The three methods are designated as the "tandem" method, the "total score" method and the method of "independent culling levels." The "tandem method" is to select for one trait at a time until that is improved; then for a second trait; later for a third, etc.; until finally each has been improved to the desired level. The "total score method" is to select for all the traits simultaneously by using some index of net merit constructed by adding into one figure the credits and penalties given each animal according to the degree of its superiority or inferiority in each trait. In the method of "independent culling levels" a certain level of merit is established for each trait, and all individuals below that level are discarded, regardless of the superiority or inferiority of their other traits.

In order to select most efficiently, the following things need to be known for each trait which influences practical value: (1) The amount by which each unit of variation in it actually raises or lowers an individual's practical value (relative economic value of the trait); (2) the extent to which observed variations in it represent differences in genetic constitution (its heritability); and (3) the genetic and environmental correlations of each trait with the others. The method of total score is most efficient, while the tandem method is the least efficient of the three. The reasons for that and the extent of it will appear in what follows.

Relative Economic Value

Finding the relative economic value of each trait is the first step in framing the ideal toward which the breeder is to strive. This will need to be done separately for each kind of animal or product and may well vary from region to region, or even from farm to farm in the same region, and from one time to another whenever there are relatively permanent shifts in market demands. An example is the finding by Winters[2] that one pound of wool is worth 3.4 pounds of lamb. In the present article, a with appropriate subscripts will indicate the relative economic values for the different traits. Thus in Winters' example if wool is the first characteristic and lamb is the second, then a_1/a_2 equals 3.4 if both are expressed in pounds.

The efficiency of different methods of selection can be compared by multiplying the improvement expected in each indi-

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vidual trait by its relative economic value. Thus, the *aggregate* genetic gain expected from selection by a given method is

$$\overline{H} = a_1\overline{G}_1 + a_2\overline{G}_2 + \ldots + a_n\overline{G}_n \quad (1),$$

where the G's each represent the amount of genetic improvement expected in that trait.

Heritability

The observed trait (X) is the result of the combined effects of a number (usually large) of genes and of innumerable environmental factors. Let G for each individual be the sum of the *average* effects of all its genes which influence the expression of that trait. G is thus the genetic or breeding value of that individual in that population. Then,

$$X = G + E \quad (2),$$

where E represents the combined effects of all factors which make G and X unlike; that is, differences due to dominance, to epistasis and to environment. For convenience, G, X and E are all expressed as deviations from the population mean. Then from (2), the observed variance (σ^2X) in the population is

$$\sigma^2 X = \sigma^2 G + \sigma^2 E \quad (3),$$

if G and E are uncorrelated, as would be the case unless there is some consistent tendency for better-than-average genotypes to be exposed to better or worse-than-average environment. From (3) we have

$$g^2 = \frac{\sigma^2 G}{\sigma^2 X} \quad (4),$$

where g^2 represents the heritability or the fraction of the variance in a given trait which is due to the additive effects of genes. Lush[1] discussed methods of estimating heritability in farm livestock.

Selection for one Trait at a Time

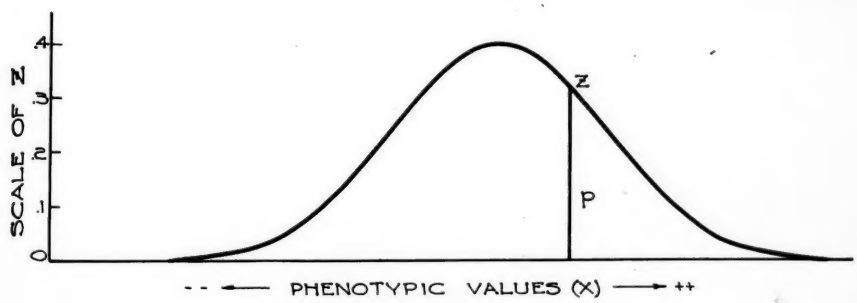
The amount of selection actually practiced is more difficult to measure in herds of domestic animals than in most crop plants because generations overlap, culling is practiced at many ages, etc. To facilitate calculating the intensity of selection, the following simplifications were introduced: (1) Selection is practiced at only one stage of the life cycle; (2) the generations do not overlap; (3) all individuals below a minimum level of desirability are culled without exception; and (4) selected individuals have equal opportunity to leave offspring. Selection under these simplified conditions is illustrated for a normally distributed population in Figure 11.

The genetic gain in the selected group (the genetic average of the selected group minus that of the unselected group, or the phenotypic average of the offspring minus the phenotypic average of the generation in which their parents were born) is expected to be

$$\overline{G} = \frac{z}{p} g^2 \sigma_X \quad (5),$$

where z is the height of the ordinate of the normal curve at the lowest value of X retained.* The proportion which must be saved (p) depends on the reproductive rate and longevity of the species under consideration and upon whether the population is expanding, stationary or declining in numbers. The ordinate (z) of the normal curve is determined by the intensity of selection (p). Values of z for corresponding values of p are given in many statistical reference books. The amount of progress is expected to be larger as p becomes smaller; that is, as selection becomes more intense. The relation is not linear, although it is nearly so from $p = 1.0$ to near $p = .3$. When p becomes less than .3, the amount of progress expected per unit of further decrease in p increases at an ever-in-

*Some additional gain is to be expected if epistatic effects exist, but that is temporary and is not considered further here. Such gains tend to disappear in succeeding generations as the special gene combinations which produced them segregate into others.



SINGLE-TRAIT SELECTION
Figure 11

A normal distribution of phenotypes showing how a population could be separated sharply at a given point into a selected fraction (p) and a remainder which are culled.

creasing rate. The term g^2 appears in equation 5 because it is a measure of the accuracy with which animals having the highest genetic values can be chosen by selecting directly for phenotypes, i.e., of the regression of genetic values on phenotypic values.

In the method of tandem selection, differences in the a values would lead to the most important traits being selected for perhaps three or four generations, while the less important ones would be the object of selection for only one or two generations in each cycle of improvement. In the extremely simple case in which n characteristics were independent and equally important, the *average* improvement per generation in each would be only one nth of the improvement which would be made if it were the sole object of improvement over the entire period.

Selection for a Total Score

The total score method will permit extra merit in one characteristic to offset slight defects in another. By its use individuals with very high merit in one characteristic are saved for breeding even when they are a bit inferior in other characteristics. This does not happen when the method of independent culling levels is used. An example of such a score or selection index is that currently being used in the swine breeding experiments at the Iowa Agricultural Experiment Station for selecting young boars and gilts. An index (I) is calculated for each pig, based on its own weight at 180 days (W), its score for market desirability at 225 pounds live weight (S) and productivity of its dam (P) as follows:

$$I = .5W - .06S + P.$$

Each pig is given additional credit or penalty for the average weight and score of the litter in which it was born (weighted according to the reliability of the litter average) after litter records are complete.

The greatest practical obstacle to the total score method is the difficulty of knowing how much importance should be given each trait in making up the score. The gain in each trait depends partly upon the heritability of variations in that trait (equation 5) and the aggregate gain is the sum of the products of the gains in individual traits and their relative economic values (equation 1). Evidently, both the heritability and relative economic value of a trait should influence its weight in making up the total score, since both contribute to the aggregate gain. Only one combination of weights allows maximum aggregate gain for a particular set of traits, just as only one combination of regression coefficients allows maximum accuracy in predicting a dependent from a set of independent variables.

If the traits are uncorrelated genetically or environmentally, the correct

weight for each trait in making up the score is in proportion to the product of its economic value and heritability (ag^2). When each of n uncorrelated traits is weighted thus, the aggregate genetic gain is a maximum for any culling level. The aggregate gain expected from selection directly for total score is

$$\overline{H} = \frac{z}{p}\sqrt{a_1^2 g_1^4 \sigma_1^2 + a_2^2 g_2^4 \sigma_2^2 + \ldots + a_n^2 g_n^4 \sigma_n^2} \quad (6).$$

In practice, however, some of the traits are likely to be correlated, either because some genes affect two or more traits (pleiotropy) or because the same environmental circumstances affect their developmental processes. Making the weights proportional to ag^2 for each trait is perhaps as good an approximation as can be made until the genetic and environmental correlations are known. But these correlations, if high, may alter the correct weights in an unpredictable manner, just as the regression coefficients in a multiple regression equation (of which general situation this is a particular case) may be changed considerably by the correlation between independent variables.

Independent Culling Levels

When independent culling levels are established for several traits, culling heavily for one trait limits the amount of culling which can be practiced for others. A culling level set too high for a trait which is low in heritability or of small economic importance automatically lowers the intensity of selection which can be practiced for other traits. Only one combination of culling levels, determined by the heritability and economic importance of the traits and by p, the total fraction retained, permits the aggregate genetic gain to be a maximum. For n uncorrelated traits the genetic gain expected from selecting independently for each trait is

$$\overline{H} = a_1 g_1^2 \frac{z_1}{q_1}\sigma_1 + a_2 g_2^2 \frac{z_2}{q_2}\sigma_2 + \ldots + a_n g_n^2 \frac{z_n}{q_n}\sigma_n \quad (7),$$

where the q's refer to the fractions saved for each different trait. In this case,

$$q_1 q_2 \ldots q_n = p$$

The product of the relative economic value (a), heritability (g^2) and standard deviation is a measure of the importance of a trait in the selection program. These values must be known in order to find the culling levels for the various traits which make H a maximum. The procedure of finding the best culling levels for several traits which differ in importance is rather tedious. Different values of q (with corresponding z), subject to the restriction that $q_1 q_2 \ldots q_n = p$, are substituted into equation 7 until that combination is found which makes H a maximum.

Table I shows the values of q_1 and q_2 which make H a maximum for certain selected values of p and where the importance of two traits varies. When the traits are equally important (line 1), the same culling level ($q_1 = q_2 = \sqrt{p}$) for each trait is most efficient for every value of p. When one trait is twice as important as the second (line 2), the percentage culled for each trait should be 19 and 1, respectively, if 20 per cent of the total can be culled ($p = .8$); but 76 and 18, respectively, if 80 per cent of the total can be culled ($p = .2$). The relative amount of culling which should be done for the least important character increases as p decreases. However, the two lower lines indicate that even a slight amount of culling for the trait of lesser importance may be too much if the traits differ widely in importance. These figures show vividly the danger of doing real harm to a breeding program by allowing minor points any appreciable weight in selection. This is the real basis for the quarrel between "fancy points" and utility breeding.

Comparison of the Three Methods

The efficiency of the three methods can be compared directly for the special case in which the n traits are independent and the products of the relative economic value, heritability and standard deviation for each trait are equal. Otherwise the formulae remain complex. Under these simplified conditions, the expected genetic gain due to one generation of selection for one trait alone may be written (from equation 5)

$$\overline{H}_1 = ag\frac{z_p}{p}\sigma.$$

That due to selection for a total score based on n traits is (from equation 6)

$$\overline{H}_2 = \sqrt{n}ag\frac{z_p}{p}\sigma.$$

For the method of culling levels the expected genetic gain is (from equation 7)

$$\overline{H}_3 = nag\frac{z_3}{q}\sigma,$$

where z_3 is fixed by q, the common culling level for all traits, and $q = n\sqrt{p}$.

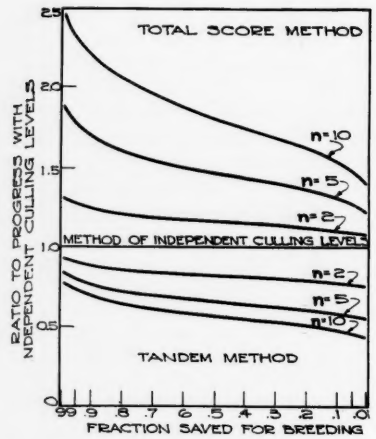
The ratio of H_2 to H_1 is $\sqrt{n}$, indicating that the total score is $\sqrt{n}$ times as efficient as the single trait or tandem method, regardless of the intensity of selection. A geometric analogy may make clearer the reasons for this superiority. In a square the distance from one corner to the opposite one along the sides, is $\sqrt{2}$ times the diagonal connecting the two corners, and in a cube the distance along the three sides is $\sqrt{3}$ times the diagonal connecting opposite corners. That the same principles extend to cases in which more than three characteristics are considered can be visualized by considering each side of the square or cube as being itself a compound score for two or more characteristics. The progress (distance) in *any one* trait (direction) is only $\frac{1}{\sqrt{n}}$ times as great by the total score method as if selection were applied for that trait alone. This latter fact is probably the basis for the popular belief that selection is most effective when applied to only one trait at a time.

When the traits differ in their importance but are still independent, the geometric analogy can be extended to rectangles and rectangular prisms with the lengths of the sides proportional to the importance of the traits. The total score method is more than $\sqrt{n}$ times as efficient in those generations when the tandem method is being applied to traits of minor importance and is less than $\sqrt{n}$ times as efficient in those generations when the tandem method is being applied to traits of more than average importance.

The method of independent culling levels is always intermediate in efficiency between the other two if each is compared at the maximum efficiency possible for that method. Figure 12 shows the effect of different values of p upon the relative efficiency of the three methods for two, five and ten equally important, uncorrelated traits. Progress by all three methods is larger with lower values of p but this increase is more rapid under the method of independent culling levels than in the other two; hence the downward trend of the lines indicating *relative* efficiency of the others. The relative efficiency of the independent culling levels method is closer to that of the tandem method when the selection is very mild, but comes closer to that of the total score method when the selection is very intense. It is a little greater than indi-

TABLE I.—The proportions which should be saved in order to make maximum genetic progress when independent culling levels are used for each of two traits

$\frac{a_1g^2_1\sigma_1}{a_2g^2_2\sigma_2}$	Total Fraction Retained (p)					
	.8		.5		.2	
	q_1	q_2	q_1	q_2	q_1	q_2
1	.89	.89	.71	.71	.45	.45
2	.81	.99	.53	.94	.24	.82
4	.80	1.00	.51	.99	.21	.98
8	.80	1.00	.50	1.00	.20	1.00



METHODS COMPARED

Figure 12

Efficiency of total score method and of tandem method, relative to the method of independent culling levels, where all n of the characteristics are uncorrelated and equally important.

cated in Figure 12 if the traits differ in importance.

The method of independent culling levels has one practical advantage over the total score method in that animals may be culled for each trait whenever that trait becomes evident, without waiting until all the traits can be measured.

Discussion

In all three methods there is always the danger that selection will fall below its maximum efficiency because too much attention is paid to some characteristics and too little to others. In the tandem method that would take the form of selecting first or in too many generations for unimportant things while postponing or selecting too briefly for more important things. In the total score method that would take the form of using too high values of a for some characteristics and too low values for others, or making mistakes in estimating g^2 so that some characteristics would be thought more highly heritable and others less highly heritable than they actually are; or of failing to consider properly the effects of genetic and environmental correlations between traits. In the method of independent culling levels, the culling level might be set too high for one characteristic, too low for another. The figures in the bottom lines of Table I will show how real this danger is. It cannot be emphasized too strongly that increasing the intensity of culling for one characteristic automatically lowers the intensity of selection possible for other characteristics, if management and reproductive rates remain the same. It is not apparent that one method is more subject to error from this source than the others are; we have not investigated this in detail.

The values of $\frac{z}{p}$ given in statistical tables are for *normal* curves, whereas biological material is often skewed a little. Skewness is not likely to be important for a characteristic as complicated as net merit. When the population is skewed with the long tail of the distribution toward low merit, progress is faster with mild selection and less rapid with very intense selection than in a truly normal curve. If the long tail of the distribution is toward high merit, the reverse is true—progress is a little less with light selection but a little more with intense selection. The type and extent of skewness found in actual populations seems unlikely to affect seriously the relative efficiency of the three methods.

Selection as actually practiced is usually a combination of the second and third methods except that neither the culling levels nor the score are very definite. Some animals very poor in one or two traits are culled while still young and before their other traits have developed. Some selecting may be done on pedigree, contemporary relatives or progeny. (These may be considered as additional traits in the preceding discussion and formulae.) Finally, the selection process

may be conditioned largely by animal health (which affects p) and by the breeder's ability to measure or observe individual merit for the important traits and to weigh the different traits according to their relative importance. The breeder's carelessness or inability to observe correctly would cause those selected and those culled to overlap somewhat in X, instead of being as distinct as indicated in Figure 11. That would bring the mean of the culled and selected groups closer together so that progress would decrease, apparently as much (relatively) with one method as with another.

The rate of genetic progress may be increased when heritability is low by adopting some criterion of selection other than the individual's phenotype, or by mating systems other than that of random mating of animals selected upon the basis of their phenotypes.[3] These supplementary methods serve to increase the correlation between the genotype and the criterion of selection, so that fewer errors are made due to the deceiving effects of dominance, epistasis or environmental factors. This leaves the relative efficiency of the three methods unchanged.

Conclusions

Selection for a total score or index of net desirability is much more efficient than selection for one trait at a time. A total score based on n equally important, uncorrelated traits is $\sqrt{n}$ times as efficient as tandem selection for the same traits, one at a time. The progress made in any one trait by the total score method is only $\frac{1}{\sqrt{n}}$ times as much as if selection were directed at that trait alone.

Selection for several traits by using independent culling levels for each is more efficient than tandem selection for each trait one at a time, the relative efficiency increasing with the number of traits and intensity of culling. Selection on independent culling levels is less efficient than selection on total score but in some cases permits earlier selection without waiting until all traits are mature.

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◆

"FACTS OF LIFE" FOR SOCIOLOGISTS

Another Chapter in the Biological Alice-in-Wonderland

AS the corpus of human knowledge grows more complex, its integration and interpretation becomes increasingly difficult. A point is reached when only a super-genius can do justice to any broadly-based discipline. He must not only have a huge subject-matter at the tips of his mental fingers, but he must also be a master of exposition, if he is to capture the minds of his audience. Super-geniuses are rare enough so that recourse may be had to such makeshifts as the symposium. At its best a symposium contributed to by the ace minds of a subject can be extremely valuable, as witness such editorial labors of love and erudition as the symposium which summarizes our knowledge of the sex-hormones. But symposia can do more harm than good if the choice of authors is not happy, and if the editor does not succeed in attaining accuracy, continuity and integration. Such difficulties seem to cover the basic failings of a recent ambitious attempt (711 pages) to put sociology on a broad and solid basis.* Many biologists will echo a loud

*PENDELL, ELMER, Editor. *Society Under Analysis.* 21 Cooperating Sociologists. Pp. viii+711. $4.00. The Jaques Cattell Press, Lancaster, Pa. 1942.

"amen" to the need for this, and to the Editor's preface which gives us hope that the job may have been done.

> This book had its inception in the conclusion that the time has come for a closer rapport between the physical sciences and the social sciences. In the fact that geographic and geologic phenomena, physical laws and chemical uniformities, heredity, and economic probabilities, as bases for human behavior have been neglected in most sociology classes we perceived an appropriateness in making available a text which would maintain a balance of attention to (1) relationships within the social structure and (2) relationships of that structure to the non-institutional factors that furnish the matrix for the structure. . . . The editor asked of the authors that treatment be restricted to objective analysis. . . .

This surely sounds most hopeful. But it is significant that the editor makes no claim that his authors are especially qualified to write on the subjects they discuss, only that they "constitute a cross section of American Sociologists."

The reviewer is going to limit his discussion to two of the twenty-six chapters, as these deal primarily and secondarily with the biological and genetic foundations. Possibly the inaccuracies and omissions cited therein are made up for by surpassing treatment of other fields. But it would still be true that the basic biological foundations of sociology have been "done wrong by," and this could not possibly be righted by excellences of other subject-matter.

The first of these chapters is the worst. It is written by a Professor of Sociology of a Normal College, and is titled "Influence of Non-Human Organisms on Social Life." For a book put as a college text this chapter contains some passages that approach an all-time low in the bed-time-story Peter Rabbit school of "objective analysis." After explaining that we should not be ashamed of our humble relatives, the chimps and the fishes, because "very humble beginnings lead to very great ends," we come upon the arresting subhead and text (Capitals *not* reviewers):

MOTHER NATURE

Nature Holds the Stakes

The name mother is quite appropriate in that she is the original source of all life and being. In addition she is, like a true mother, impartial. In any argument with physical nature or between human nature and non-human factors Mother Nature holds the stakes. She can't lose.

* * *

Not only is Mother Nature impartial, but she is also neutral in the gigantic struggle that goes on for survival. The interplay of the forces of nature creates stress and tension causing dislocations which can be balanced only through struggle and conflict. All life must take part in the struggle to survive, to gain a foothold, to perpetuate its kind. The virility of life has been strikingly demonstrated by planting grain after it had lain dormant in the tombs of the Pharaohs for many centuries, and having it germinate and grow.

It is probably never quite fair to quote out of context, but space is limited, and this is frankly chosen as an outstandingly horrible example. Imagine a competent biologist, seriously undertaking to summarize the facts of life, actually being guilty of doing a Gillette Burgess, capitalization and all! And it surely is the responsibility of an editor of a text allegedly for use in college classes in sociology, to find authors who are at least casually acquainted with the field they undertake to discuss. One does not even have to be a biologist to know that stakes are held only in wagers, not in arguments and very rarely by Mothers, who are more interested in the welfare of their offspring than they are in "never losing." That the hoary and oft-exploded myth of the viable wheat from Egyptian tombs should top these other delightful fairy-tales is indeed a pleasant surprise. If this be objectivity, surely the time has come to go back to Santa Claus.

There is plenty more. This for in-

stance: "The tremendous import of this is startling when you consider the possibilities among the faster breeders — rabbits, pigeons and the like. The common oyster lays about sixty million eggs." The pigeon lays hers in clutches of two; a rabbit has 6-10 young in a litter. The author ought to make up his mind about what he considers "fast breeding." "An albatross can cover the distance between New York and San Francisco in twelve hours." *Vuss you dere, Charlie?* The reviewer is still betting on Capt. Hawkes or his successors, and he has found none of his ornithologist friends who will bet on any bird flying as fast as 200 miles per hour even for short distances let alone averaging 200 miles per hour from sunrise to sunset. This should be fun for the bacteriologists: "The chills and fevers accompanying most germ diseases are due to the incubating period of the particular baby germs." The reviewer wonders whether albatrosses bring baby germs? Do they have pink and blue stockings so that their proud papas and mamas can peer into the pram and tell which takes after which? And then we suddenly become astonishingly cautious: "The pollen of certain plants is supposed to cause hay fever and other respiratory disorders in some people that are allergic to them." Here's one chap the immunologists aren't going to fool with their newfangled ideas, he just does not believe it. And this is what the bacteria are up to when they aren't exclaiming over newly-arrived junior: "They ripen cheese and vinegar and leaven the yeast and curdle the milk which makes it digestible." Fun to think how much soda bicarb it would take to settle a tummy loaded with yeast from a batch which a careless radio nostrum vendor had forgotten to have leavened. And at last reports rennet, an enzyme, was still curdling milk for digestive purposes and for the cheese industry too.

There is a paragraph headed "Eggs and Egg Products." After paying its respects to the industrious U. S. hen's two billion dozen eggs a year, it concludes: "We also rob and exploit plants as well as animals to 'make us bread.' We squeeze the juices of fruits and vegetables and grains and berries to make us jellies, jams, wines and beer . . . and we take the juice of the pine to make turpentine to adorn our homes and furniture and we grow the rubber to ease our auto rides on this too, too solid earth." So not only hens lay eggs: turpentine trees, and authors do too, apparently. And under "flavoring substances and other commercial extracts" we find strange bedfellows indeed: "vanilla, spices, peppermint, beeswax, cod liver oil, honey, pituitary extract, testicular extract, pancreatic extract and ox-gall." The spice of life, some of 'em. But more than enough. Surely nowhere else in a textbook purporting to deal with biology, could a more strange and varied collection of facts and fancies be found. And this is the "objective analysis" on which it is proposed to build the conceptual structure of the next generation of sociologists!

But let us leave Ma Nature chasing the albatross of fact and go to chapter two of the biological Singularities, parden, "Regularities," which is subheaded "Influence of Man's biological heritage in Social Behavior." This is a heavily loaded chapter in the sense that it is a résumé of the author's point of view rather than a discussion of relevant materials covered by the chapter heading. It is mostly devoted to a survey of cultural anthropology (to which an earlier chapter is devoted) and to comparative psychology. There is the shad instead of the oyster as an example of quick breeding, and considerable discussion. There is a thoroughly unsatisfactory smattering of genetics, summarized in seven propositions which could not possibly give the student any inkling of genetic processes. As an example, the first of these is as follows:

1. "The general mechanism of heredity is the same for plants and animals including man. Therefore, conclusions drawn from experiments on plants and animals seem valid for human heredity."

Such shotgun obiter always make the geneticist's hair stand straight up on end. In general no geneticist is prepared to transfer conclusions, based on experiments on rats, to mice, let alone from plants to men. This hazardous procedure has already muddied a great deal of water. Some parallels hold and some emphatically do not, and only the qualified specialist is able to assay any particular situation. To take an example, sex-linkage was first observed in man over a century ago, and the mechanism was explained in laboratory experiments with drosophila about 1910. The same phenomenon was found in laboratory mammals, and (reversed) in the hen. There is adequate ground for postulating that the same underlying mechanism is operative in all these organisms.

Under the "Significance of Human Genetics" we read: "Man can claim no immunity from the general laws of the universe, much less from those in the narrower field of genetics. Genes show an amazing stability, and outside of a few minor mutations in plants and some lower animals, induced by controlled stimulation of heat, chemicals, or electricity, gene mutation is exceedingly rare." This gives a wholly false picture of the mutation process, which goes on continuously in all organisms where controlled studies have been made. Every gene appears to have its own natural mutation rate. Haldane's estimate that the hemophilia mutation rate would give us 40 new foci each year in the United States surely makes mutation a factor which cannot be dismissed as nonexistent.

Dr. Castle's review of Stockard's report on his dog crosses (J. HERED., July, 1942), discussed the dangers of just the kind of ad lib reasoning which our author implies is the stock-in-trade of the geneticist. It is important that the student of sociology have a general idea of the methods and basic concepts of genetics. These he could not possibly get from this chapter. Surely less talk about the inheritance of social tendencies and "biological vice" and more about the *facts* which the editor promised, would have been a greater service.

The discussion of the inheritance of mental traits is most disappointing. All that is claimed is that since physical traits are inherited, mental traits must be too. The reader is given not an inkling that any direct evidence exists which bears on this crucial question. There is no mention whatever of the well demonstrated correlation of about .5 between parents and offspring with respect to mental traits just as there is with physical traits. Studies of identical and fraternal twins, especially identicals reared apart, and studies of foster children are all completely ignored. Surely these three lines of evidence all consistently give at least a first approximation of the limits of heredity and environment in the development of human intelligence. But the student is told nothing about any of them. It is absurd to pretend that the subject has been adequately surveyed in the presence of such glaring lacunae.

As a sociological document, setting forth at length what a "cross section of American sociologists" think about mankind and the universe, such a symposium is important. Perhaps it would have been a good idea to analyse the responses and write a book discussing the longcomings and shortcomings of sociological points of view than to publish the essays themselves. As far as the biological chapters are concerned, they do not support the publisher's claim made in an advertising circular, that "twenty-one eminent sociologists" have produced a book whose "logical arrangement and comprehensive treatment of the subject constitutes an ideal text for elementary classes in sociology. It is thoroughly up-to-date, authoritative and distinct in its orientation." Better than that, its biology is unique. It is sad to think that there will be at least 21 classes each year in which the embryo sociologists of America will learn of "logical arrangements" where rubber trees lay eggs, and bacteria go wortling through the yeast, a-leavening as they go.—R. C.

A NEW MAP OF THE SALIVARY GLAND 2L-CHROMOSOME

of *Drosophila Melanogaster**

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Department of Zoology, Columbia University, New York, N. Y.

THE present map is the fifth and last in the series of revisions of the salivary gland chromosome maps of *Drosophila melanogaster*. Preceding this map of the 2L-Chromosome, were revisions of the *X* (this JOURNAL, 1938)[2], of 2R (1939)[4], of 3L (1941)[5], and of 3R (1941)[6]. All of these maps serve as supplements to the original map published in 1935[1], each one retaining the divisions and subdivisions substantially as in that map, with the few necessary changes indicated by broken lines. The fourth chromosome, the shortest of the complement, has not been revised, as the original drawing in the 1935 paper is correct as it stands.

Permanent aceto-carmine smears of larval salivary glands, prepared by Bridges' vapor replacement method, were the material used for the entire series of revisions. For the present map, chromosomes were selected for favorable conditions of stretching, and a minimum of eight camera lucida drawings for each section was made from them at a magnification of 5,000 diameters. The revision consists of a generalized composite of these drawings, its dimensions being averages of their lengths and widths with the individual bands filled in by comparison of all the drawings. The final number and character most closely compatible to the information given by all of them was taken as the standard for the maps. Many more bands than those indicated in the 1935 maps have been included in the revision and the characterization of the bands has been improved.

The present limits of the major divisions, as marked on the 1935 map, have been retained in all but two cases, these two being shifts in the beginning of sections 28 and 39, and the subdivisions have been retained in all but ten cases. These shifts were made primarily to make use of heavier, darker bands, making some of the divisions easier to find, and secondarily to even up the lengths of the divisions and subdivisions as much as possible. Several preparations were found in which the chromocenter was complete and it was possible to map the whole of that region. Section 41 has been redrawn from the earlier 2R-Chromosome revision[4], but its bands have not been included in the band count. The 2L Chromosome thus ends with Division 40, with the spindle-fiber attachment located in the subdivision 40F, probably in the last double line, as indicated in the top line of the revision. The chromocentral heterochromatin starts with 40B1-2 and ends with 41D1-2.

The new map contains 803 bands, counting capsules as two, compared with the 584 of the 1935 map, and is 370 microns long as against the 205 of the old. Choice of larger chromosomes and use of sections of greater and more uniform stretch account for the differences in these dimensions.

The most constant features of the 2L-Chromosome are the "dog-collar" in 21C-D, the "shoe-buckle" of 25A, the "shield" in 30A, the "goose-neck" of Division 31, the "salpas" of Division 32, the dilation in 35A-B, and the heavy bands of 34E-F, 36D and 39D, which are the regions principally involved in the adhesions that usually loop the basal portions of this chromosome.

The linkage map, first line of the fig-

*This paper, as well as the preceding revisions of the salivary gland chromosome maps, was made possible by a grant from the Carnegie Institution of Washington.

ure, gives the latest revision of the gene positions, as given in *DIS* -9[8] and later issues, all RK-1's and some of the RK-2's being included. Below that is the present salivary gland chromosome revision reproduced at one fourth the size of the detailed map. Between the two as many correlations as are known of the salivary gland chromosome positions of the genes are shown. These positions are located according to the data given in the symbol list of *DIS*-9, and in the symbol list revisions of *DIS*-12[10] making use of the information on inversion, translocation and deficiency limits and inclusions, and from private communications of E. B. Lewis for genes located near the tip of 2L, and of J. Schultz for *light* and *purple*, also from the Carnegie Report[9] of V. Curry and C. B. Bridges for the genes located near *dumpy*, and from the unpublished material of C. B. Bridges for *black* and others.

The large detailed salivary gland map revision of the 2L-Chromosome of *Drosophila melanogaster* follows on the last four lines of the figure.

Size of Salivary Gland Chromosomes

Now that all the revisions are finished it is possible to make comparisons in length and number of bands with the original map of 1935, and draw some conclusions from the comparisons.

To supplement the data already obtained, measurements were made of lax chromosomes to see whether "normal" length chromosomes were related in any way to the stretched lengths of the original and revised maps. Slides were made of larval salivary glands which were smeared just enough to break open the nuclei, without stretching the chromosomes. As many complete nuclei as possible were selected, and enough partial nuclei, with at least four of the six arms present, were added to bring the total number of examples up to approximately fifty for each chromosome. Camera lucida drawings were made of these nuclei, and the lengths of the chromosomes were measured.

Table I gives the average and range of chromosome lengths for the nuclei of five different wild type female larvae, the average and range of the whole group, and the average of the means of the individual larvae. The data indicate that there is no significant difference among individual larvae grown under similar conditions to the same age, though the larvae are from five different strains. There are no great differences among the four medium length chromosomes which are all about the same length in the lax nuclei, differing very little from nucleus to nucleus. Chromosome 4 is the very short one, and 3R is the longest of the six, markedly so in all the nuclei.

Figure 14 shows histograms of the length distributions, which are quite compact, and fairly normal, curves. The spread in general is due to differences in absolute chromosome size, as all the chromosomes of one nucleus vary in the same direction. This is only generally and not strictly true, as often one or two chromosomes may be markedly out of the average order of length in the different nuclei, which is shown by the skewness of all the distributions except that of the X-Chromosome. This can be attributed to the fact that as far as possible complete nuclei were chosen which means that some of the chromosomes measured were ones which were disproportionately stretched compared to others in the same nucleus, and hence show up in the distributions by tailing off to the left.

The X-Chromosome is the most uniform and compact, which I think can be attributed to the fact that there are more heavy double bands in this chromosome, as Table II shows. This prevents it from being stretched as much as the others. While the bands are in general inelastic, and most stretching comes in the clear areas between them, the bands are somewhat stretchable, and the more so the lighter they are, so that the difference is enough to explain lack of stretch (or rather difficulty in stretching) in a chromosome full of heavy double bands. Table III shows that the X does indeed have more bands per unit than the others

DROSOPHILA
MELANOGASTER

LINKAGE MAP

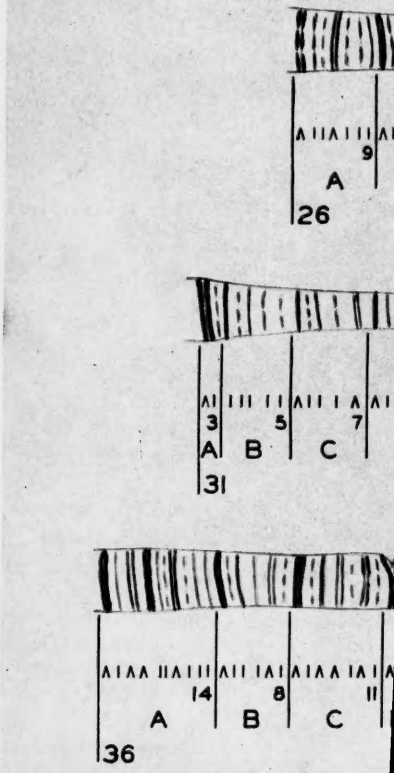
SALIVARY MAP

SCALE = 10μ

SALIVARY
2L - CHROMOSOME

SCALE = 5μ

BAND CHARACTER
LINE NUMBERING
SUB - DIVISIONS
DIVISIONS



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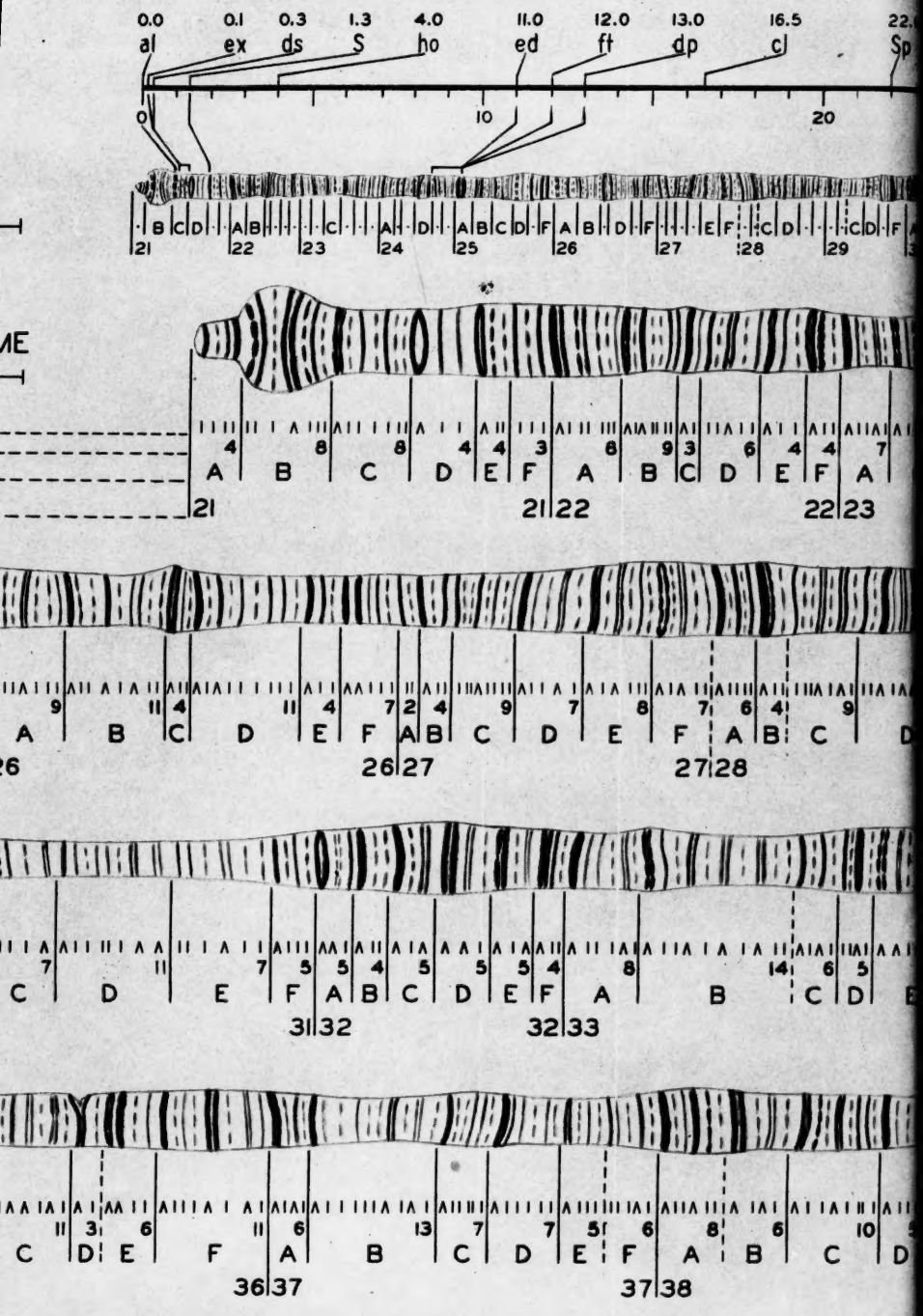

of Heredity, Vol. 33, No. 11, November, 1942. (To follow page 404.)
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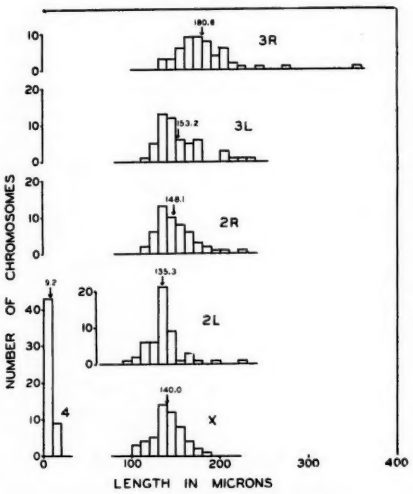
SALIVARY GLAND 2L CHROMOSOME OF *DROSOPHILA MELANOGASTER.*

Figure 13



LENGTH OF CHROMOSOMES

Figure 14

Length of a sample of approximately fifty unstretched chromosomes from five larvae. The distributions are consistent enough to give high validity to conclusions based on averages.

do, which may be due to not having been stretched as much.

The distributions of chromosome length are similar enough, and normal enough, so that their average lengths are valid bases for conclusions which will be consistent for all chromosomes.

Table II compares lax length with chromosome length in the original map and in the revisions. The amount of stretch in the latter two over the lax length is proportionately very uniform, all the chromosomes remaining in approximately the same order, and increasing about the same percentage. The lax length chromosomes are about a hundred times as long as gonial chromosomes, with the 1935 map chromosomes half again as long. The revisions are about twice as long as the 1935 map, three times lax length, and three hundred times gonial length. The second part of this table gives the number of bands in the 1935 map, and in the revisions, with a column of band counts in which the doubles are counted as one. The increase in number of bands from the 1935 map to the revisions averages about 1.6 times, while the increase in length is 2 times. The increase in number of bands is not uniform from chromosome to chromosome, nor do any of them double the number of bands. These facts indicate that the revisions are stretched enough to resolve practically all the bands and that further stretching will not reveal more. That is, the maximum number of bands has now been reached in the revisions and the stretching has gone beyond the point where it is possible for more bands to be resolved and doubles separated.

Relation of the Genes to the Bands

The doubles-counted-as-one count was made in an attempt to see whether there is any relationship between length of chromosome and gene number, it being thought that doubles indicate one locus, and hence such a band count would give the number of loci. The result of this count is 3,795, which does not deviate too greatly from the estimate of 3,000 genes for the animal, and is closer than the 5,072 total band count. However, the latter is not so much greater that any conclusions can be drawn as to whether double bands equal single loci. Table III gives a comparison of band densities, which shows that in general the X-Chromosome has more bands per unit length than the others (except the revised 2R-Chromosome), and that the densities for each chromosome remain fairly uniform, whether lax length, revised length or even 1935 length be used, which would be expected from the fairly uniform stretch shown in Table II. This relationship changes only when the doubles-counted-as-one comparison is used, the other chromosomes increasing their band density as compared to the X-Chromosome, which means that the X has more double bands than the others, as was noted above in the discussion on stretching.

In general the X-Chromosome has been found to contain more genes than

the other chromosomes (although this is possibly only an apparent difference, as sex-linked genes are easier to pick up). It would seem that the comparison of total band count to length, rather than the comparison of doubles-equal-to-one count to length, would give a better indication of the relative frequencies of the genes. If this is so, the total band count would be a closer approximation to the number of genes, and each band represents a band locus and doubles must then be two loci. However, this conclusion needs supporting evidence.

The doubles-counted-as-one count shows that each chromosome differs in the number of doubles, and that the number of doubles is not proportional to the chromosome length. These facts indicate that doubles are real, characteristic features of the chromosomes, and not separation products of stretch, as is assumed in the theory that all bands are double and are resolved by excess stretching. The fact that excess stretching does not bring to light any more doubles than those already found under moderate stretch supports the idea that they are characteristic features. Chromosome breaks have not been found between the halves of doubles, nor has more than one gene been located in any double. This supports the supposition that doubles, which are real features, as discussed above, are duplicated loci,—that is, simple band repeats. If this is the case, then each double contains two similar loci. This would explain why they can behave like single gene loci and yet give a relative band count (although not total band count) frequency as though they represented two loci each.

E. B. Lewis[7] has obtained some evidence at the *Star* locus that doubles are duplicated loci. He has found that *Star* and *asteroid* are both in the double band 21E1-2. One is in one band and the other in the other band, with a very small amount of crossing-over between them. These two genes act as allelomorphs in opposite chromosomes, but interact with considerable position-effect when in the same chromosome. If the original *Star* (wild type) locus were duplicated to form a double band repeat. there would then be a doublet containing two similar loci, as postulated above, which would apparently act as a single locus as far as locating genes in the band is concerned. Subsequent mutation of one half of the double to *Star*, and the other half to *asteroid* at some other time, would bring about the situation Lewis found. That it is possible to break the chromosome between the halves of a double is shown by his small recombination percent, although the possibility must be extremely rare, as no other cases are known.

C. B. Bridges[8] found that two regions of the 2R-Chromosome containing the same number of bands, and of the same genetic map length, differed by a factor of five in the number of genes contained in that distance, and postulated that the lower coefficient of mutation was in the region containing the most repeats (and hence containing masking gene duplications) some of which were observed. It can be postulated that many of these repeats are in the form of double bands, and hence that regions rich in double bands should show a low coefficient of mutation. This is indeed true in all but the *X*-Chromosome, with the greatest number of double bands and yet many genes. This would seem to contradict such an assumption unless it can be shown that the *X* represents a more advanced state of chromosome evolution in which more of its duplicated loci have mutated to genes different from the parent genes. The *X* seems to have fewer long repeats than the other chromosomes, which might be enough to give it more different loci in spite of having more double bands.

Repeats

The presence and importance of repeats in the evolutionary history of the chromosomes of Drosophila have been thoroughly discussed by C. B. Bridges in two papers [1, 8], and by other authors. Repeats of all lengths, from doublets to whole sections, both direct and symmetrically reversed in tandem, inserted

in the same and other chromosomes, have been observed in the whole chromosome complement of *Drosophila melanogaster*. The evidence for their presence comprises general appearance, the folding back into synapsis of reversed repeats, and the synapsis of bands from one chromosome with those of other sections of the same or different chromosomes.

In general, these repeats can be divided into two classes, "real" and "apparent,"—real when euchromatin is involved and apparent when heterochromatin is involved. These two classes can be distinguished in that euchromatic repeats can be of any length, and can contain bands of all intensities, and usually exhibit only weak and occasional synapsis. The apparent repeats always involve very heavy black bands, limited in number, and exhibit strong and constant synapsis. This latter type is actually only the general manifestation of the non-specific attraction of bits of heterochromatin for each other, and occurs wherever heterochromatin has been inserted into the euchromatic arms of the chromosome. Wherever such synapsis occurs, the dark bands involve synapsis only as region to region, rather than as band to band, differing in detail from each other, the heterochromatic inserts being only roughly homologous. Often these regions are found in synapsis with the chromocenter, forming a regular heterochromatic bridge from it to one or more inserts. The partners of this synapsis may change from nucleus to nucleus, and involve different members, whereas euchromatic repeats are always constant in the partner with which they synapse, and can be matched band for band.

Most of these heterochromatic repeats are in the 2L-Chromosome, and in the basal portion of that, although one or two examples of such inserts are found in other chromosomes. The regions of 2L generally involved are the heavy bands of 34E-F, bands in Sections 35 and 36, and in 39. Attraction between them and the chromocenter causes turnbacks and loops, and the general coiling and twisting of the whole basal portion of the chromosome.

This problem of repeats will be discussed further in a later paper.

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TABLE I. Lax length, chromosome of *Drosophila Melanogaster*. Numbers in parentheses indicate number of complete nuclei. All measurements in microns.
TABLE II. Comparison of chromosome lengths and numbers of bands between the original map and the revision, including proportionate increases in length and number over the lax length, and giving band count for doubles counted as one. →

Larva	Nuclei		X	2L	2R	3L	3R	4
I	13	Mean	144.4	142.8	146.0	153.5	188.5	10.1
	(13)	Range	120-165	95-229	122-200	121-208	135-210	6-16
II	12		139.6	129.1	137.9	146.1	172.9	8.5
	(11)		125-152	102-145	118-180	116-232	133-228	6-11
III	8		148.9	131.7	161.9	155.0	201.5	9.4
	(7)		109-178	110-170	141-220	130-205	150-352	7-15
I'	16		128.1	133.1	144.0	148.1	166.9	9.0
	(7)		105-157	110-167	115-182	120-218	137-200	7-12
V	7		147.6	142.0	161.6	172.6	185.3	8.8
	(4)		115-188	130-160	130-195	128-223	175-197	8-11
5	56 (42)	Cytogenetic	53	52	53	54	54	52
Average			140.0	135.3	148.1	153.2	180.6	9.2
Aver. of Means			141.7	135.7	150.3	155.1	183.0	9.2
Total range			105-178	95-229	115-220	116-232	133-352	6-16

	length in microns			Number of bands		
	lax	1935	revision	1935	revision	doubles=one
X	140=1	220=1.57	414=2.96	725=1	1611=1.39	698
2L	135=1	205=1.52	370=2.72	584=1	803=1.37	607
2R	148=1	245=1.65	446=3.01	660=1	1136=1.72	854
3L	153=1	210=1.37	424=2.77	542=1	884=1.63	688
3R	180=1	280=1.55	519=2.88	697=1	1178=1.69	915
4	9=1	15=1.67	(15=1.67)	50	(50)	(33)
	765 = 100x gonial (7.5μ)	1175=150x gonial	2188=300x gonial	3258	5072	3795
		=1	=2	=1	=1.6	

TABLE III. Density of band numbers in the different chromosomes, taking the X as unity, including comparison of band numbers with one length, band number with lax length, and doubles-counted-as one number with lax length. →

bands-length-	1935/1935	revis/revis	revis/lax	2=1 lax
X	1.00	1.00	1.00	1.00
2L	.86	.89	.83	.90
2R	.82	1.04	1.06	1.15
3L	.79	.86	.80	.90
3R	.76	.93	.91	1.02

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Six Generations to A Century

(*See illustration, page 370*)

THE photographs on page 370 records a notable instance of human reproductivity, in a Hungarian family living at Bajosa, Hungary. The mother, Mrs. Maria Mlinarics married when she was not yet fourteen, and a baby daughter was born during the following year. This daughter married at fourteen and she in turn had a daughter in 1939. Maria will be thirty her next birthday, so that for two generations the rate of reproduction has been a little better than six generations to a century.

Very likely the war will put an end to the Mlinarics' rapid reproduction for a time, or even to the Mlinaric family permanently. Nevertheless their example might be the basis for a few comparisons. The contrast in total descendants between Maria's potential and that of a family reproducing at the rate of four generations per century is impressive. If Maria had four children at fifteen month intervals, and if her descendants repeated her pattern, each having four children, too, who survived to reproduce, she would have a total of 2,048 descendants by the 2050's. If another woman had four surviving and reproducing children on a four-generation-per-century basis, she would have 256 descendants a century hence. If Maria had four children and the slow-reproducing family had three or two, the contract would be even more startling. On the two-child basis there would only be sixteen descendants to balance against Maria's two thousand, or over a hundred to one!

To consider problems of human reproduction purely as a geometric progression does not accord with any actual situation, as no family line ever grows or declines that way. Maria's way of life may give a much lower survival rate than in the slow-reproducing group, and only surviving-to-reproduction counts in the contest of population growth and decline. Only in very exceptional situations is the theoretical optimum ever attained. On Pitcairn Island a generation after the original *Bounty* mutineers arrived, the population seems to have doubled in about seventeen years, which perhaps represents an all time recorded high for even a small group of human beings.—R. C.

✦

Feeding Laboratory Animals

A twenty-four page illustrated booklet, conveniently arranged to fit a letter size file, has been published by the Ralston Purina Company for distribution to laboratory workers. It contains a condensed résumé of the nutritional needs, breeding habits, care and feeding of most of the important laboratory animals, from hamsters to chickens. The bulletin is offered for free distribution to laboratories; copies may be obtained by writing The Purina Mills, St. Louis, Missouri.

INHERITED BREECH PRESENTATION

L. J. CARTLEDGE AND FRANCES Y. HANCOCK*

BREECH presentation, or delivery of infants by the breech at birth is, apparently, relatively unusual. Hansen[1] reports 6.7 per cent in 1,882 cases, most of them from the Lincoln General Hospital at Lincoln, Nebraska, but says that this percentage is higher than the general average which he gives as 4.2 per cent. The following points were mentioned in the discussion which follows Hansen's paper.[1] In a series of 1,294 deliveries at the Indianapolis University Hospital there were 14 per cent breech cases. This series included 31 still-births, and probably also represents considerable influence of selection on the basis of complications of various sorts. In both series mortality was higher than average. R. W. Holmes considers that flat or oblique contracted pelvis of the mother may be causal. Fred H. Falls suggests that breech is more common in the arcuate type of bicornate uterus and with placenta praevia.

Whatever the incidence and causes of breech presentation may be, we have hitherto been unable to find information bearing upon its possible inheritance. One of the family inheritance charts submitted by students in our genetics classes seems, however, to afford evidence upon this point (Figure 15). The information presented in this chart was obtained from another student, known both to the student informer and to the present writer. Her position is marked as the propositus on the chart (IV-10). The symbols on the chart are either solid, representing individuals born by breech presentation; or clear, for individuals known to have been born by normal presentation; or marked with a question mark, for those individuals for whom there is no available record as to manner of birth.

A maternal great-grandmother (I-2) of the propositus was said to have been born by breech, as were all of her children (II-2, 3, 5, 7, 9 and 11). All five of the children of her three daughters were likewise breech births. These are shown as III-2, 3, 8, 9 and 11 on the chart (Figure 15). The four offspring of two of her sons (III-13, 14, 15 and 16) were born normally. There is no record on the manner of birth of the two offspring (III-5, 6) of the third son (II-3). Three of the five individuals of the third generation who were born by breech were females, and each of these three women had either one or two known breech presentation deliveries. One of them (III-3) had in addition one son normally born, and two for whom records are not available. The second (III-9) is the mother of the propositus, and bore both her children by breech. There is no record for the second child (IV-12) of the third mother (III-11) in this group. There are thus five known breech cases, one normal birth, and four unknown in the fourth generation through the female lines.

The three sons (II-3, 9 and 11) of the great-grandmother (I-2) of the propositus had two children each. The records for type of births in one of these families are not known, but in the other two all of the children were normally born. The individual at III-2 on the chart was himself born by breech, but his two daughters (IV-1, 2) were normal presentation births. Both the father shown as III-6 and his daughter (IV-8) are unknown birth types.

Summarizing these data we find, in four generations, one, six, five, and five respectively, or a total of 17 cases of breech presentation, borne by seven mothers (of whom six are shown on the chart). The total number of individuals shown is 42, and 29 of these are descended from the first woman (I-2) here recorded as being breech-born. Among the 29 descendants there were 16 breech-

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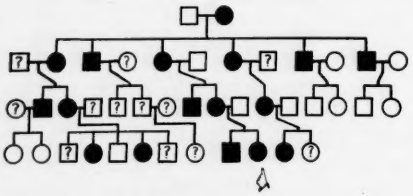

BREECH-FIRST

Figure 15

Most babies come into the world head-first, but on the average, one in twenty are born breech first. In this family, over half of all births for four generations have been by this unusual position, indicating a simple genetic basis for this tendency.

presented, seven normal, and six unknown. Descendants through the female line include all of the 16 subsequent breech cases, together with one normal and three unknown. No cases of breech presentation and only three unknowns are shown among the nine individuals descended through the male lines.

While this evidence seems to indicate that breech-born fathers do not tend to produce breech-born children, it does not offer an answer to the question which naturally comes next to mind; whether or not daughters of breech-born fathers may be expected to give birth to their children by breech presentation. That some of such daughters might show this tendency seems, from the following considerations, to be more than a mere possibility. In the first place, the presentation of infants by breech seems to be a simply inherited trait. Perhaps it is due to the presence of a single dominant gene; at least more complicated inheritance seems less likely in the family here described. That the character is expressed by the mother who bears the breech presented infant, rather than in the infant who is so born, seems to be reasonably certain, and if so, we may suppose that it depends upon some structural trait of the mother. A simple dominant factor for a structural character would be expected to be transmitted equally well through male and female lines of descent, although of course this particular character could be evidenced only in those female individuals who bear children.

It seems likely that this family shows an exceptionally high incidence of breech presentation, for even among those families in which such cases may sometimes occur they seem to be infrequent. Two cases in other families have been called to our notice, in both of which mothers are reported to have given birth to two successive children by breech presentation. However, breech presentation, with its attendant difficulty in parturition, and its somewhat higher than normal mortality, has in general been considered as an individual or accidental abnormality. That it may be not entirely so calls for careful consideration, since it would, without doubt, be of service both to the persons immediately concerned and to their attending obstetricians to know in advance the probability for this type of birth. The need for such information implies the necessity for careful study of the family history in regard to birth types, although this practice seems at the present time to be almost universally neglected. Records of maternity hospitals and the experience of individual physicians may be expected to furnish a great deal of information that could be utilized in studying the possible mode of inheritance of breech presentation.

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PROPORTIONATE DWARFISM IN JERSEY COWS

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THE literature provides numerous examples of monofactorial hereditary types that cause dwarfing in mammals and birds. Most of these mutants cause a disproportionate type of dwarfism and act as lethals or sublethals. In cattle two well-known examples are dominant achondroplasia (Bull-dog), known in Dexter cattle and studied intensively by Crew,[5] and the recessive achondroplasia found in the Telemark breed of Norway by Wriedt[12] and Mohr.[10]

Perhaps the most intensive study of the physiological action and expression of teratological genes in vertebrates is that of the Creeper and related mutant types investigated by Landauer and his associates. Landauer[7, 8] has recently reviewed the mode of action of such genes. He concludes that even while causing disproportionate dwarfism they effect the embryo as a whole. Such genes, though discontinuous in their action but teratological in nature, are not involved in the general problem of the inheritance of racial size.

It is well established that racial size is controlled by multiple factors. Castle's[1, 2, 3] serious attempt to isolate individual genes conditioning racial size in rabbits was unsuccessful. On the other hand, according to Castle,[4] some genes that condition coat color in mice, rats, and rabbits may act to slightly reduce or enhance the body size.

These color genes that influence body size are involved in racial size when color-gene differences are present. Although they have not been identified, certain other genes that are a part of the multiple factor complex conditioning racial size evidently play a more important role in differentiating hereditary racial size. These are genes for size rather than color. Evidence of a single segregating "size" gene that may be important in conditioning racial size has apparently been found in the Jersey herd of the California Experiment Station.

Our breeding work with Jerseys has been designed to fix the factors for high milk production into a more homozygous state. The rather intensive inbreeding which has been practiced has brought to light several hereditary defects two of which have been recorded by the present authors.[6, 11]

Among the progeny of one sire have occurred four individuals appreciably smaller in stature than their normal sibs (Figure 16). Those animals destined to be dwarfs as adults tend to be smaller at birth, but because their weights lie within the normal range they cannot be identified by weight, height at withers, or heart girth; nor can dwarf animals be identified by differences in general appearance early in life.

All animals identified as dwarfs were heifers sired by Gravity's Exile of Lusscroft, registration number 162551 (herd number 300C). If any dwarf males were born none was ever identified, since all males except one (347A) were destroyed at birth.

Two of the dwarf females were produced by mating 300C to supposedly unrelated cows. The other two were produced by mating 300C to his own daughters. One had a coefficient of inbreeding (Wright's[13]) of 25.78; the other of 38.67.

Body Measurements

All of the calves were raised under as uniform nutritional and management regimes as were possible to maintain. Comparisons of growth curves for weight, height at withers, and heart girth of normal and dwarf animals reveal the differences existing between the two types for each of these body characteristics (Fig-

ADULT DWARF
Figure 16

Dwarf 349 at three years of age; in the ninth month of lactation. She appears normal in every respect except that she weighs 240 pounds less than her non-dwarf half sisters.

ure 17). The key on the figure identifies each group of animals.

Since the inbred daughters of a number of Jersey sires studied by us have been found to be smaller than their outcrossed sibs (unpublished data), the mean growth of the dwarfs produced by outcrossing should be compared with the mean of their normal outcrossed sibs, while the mean of those produced by inbreeding should be compared with the mean of their normal inbred sibs.

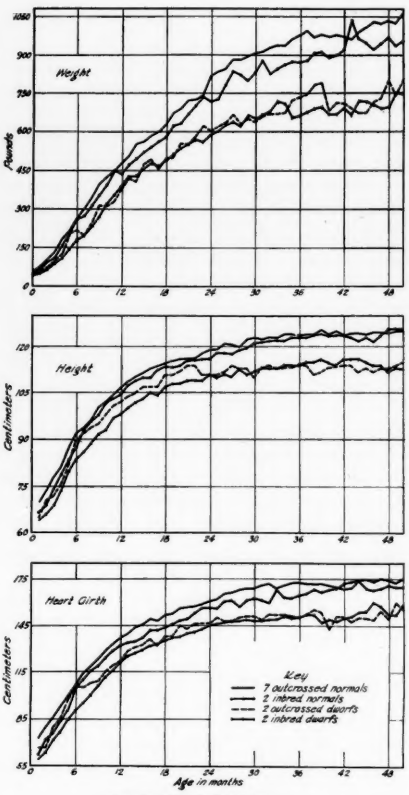
Birth weight is wholly unreliable to diagnose dwarfism since those destined to be dwarfs weigh only slightly less than the normal mean. At one month of age the heights at withers of the dwarf animals, either outcrossed or inbred, are slightly lower than the mean of their respective normal controls. The mean heart girths of both the inbred and outcrossed dwarfs are slightly less at one month than their normal half sibs. Not until the twelfth to fourteenth months do the differences in all size indices become more apparent and quite definite.

After the growth curves plateau, the mean weight of the inbred dwarfs is approximately 150 pounds less and the outcrossed dwarfs over 200 pounds less than their normal controls. In height at withers both groups of dwarfs average 10 to 12 centimeters lower than the means of their normal controls. The mean heart girths of both the inbred and outcrossed dwarfs are about 10 centimeters less than their respective normal half sibs. No significant differences in any of the size characters could be distinguished between the means of the inbred and outcrossed dwarfs. While there were individual differences among the dwarfs of both groups they were not significant.

Reproduction

Table I summarizes the data relating to reproduction of dwarfs. Most of the dwarfs were bred to their own sire (300C) and this procedure perhaps lowered their reproductive efficiency.

Outcrossed dwarf 349 was bred to her



GROWTH CURVES

Figure 17

Mean growth curves of four groups of female progeny produced by sire 300C. The dwarfs are appreciably smaller in all indices of size then their normal half sibs. Inbred normals are smaller than outcrossed normals. There is no difference in size, however, between dwarfs produced by inbreeding or outcrossing.

own sire, 300C, at 18 months of age and produced an apparently normal male weighing 54 pounds. This calf was destroyed at birth. She was again bred to 300C in 1925 and 1926 but each time aborted a female calf following a 7½ months gestation. Agglutination tests for Brucellosis were negative up to November 11, 1925, when she became positive and remained so thereafter. Brucellosis may or may not have been responsible for the abortions.

Cow 406 was bred to an unrelated sire, 320A, and aborted a male calf about five months later. She was negative to the agglutination test during this time. She was then bred to her own sire February 13, 1927. She became suspicious in her reaction to the agglutination test March 16, 1927; and definitely positive June 17, 1927. On November 6, however, she gave birth to a normal female calf (488) which lived.

Cow 460 had an inbreeding coefficient of 25.78. After many fruitless services she was placed in a pasture with sire 347A, an inbred son of 300C, and at four years of age produced a normal female calf, 519. Cow 460 was kept in the herd until June, 1933. Although bred often, she failed to reproduce again. She was negative to the agglutination test at all times.

Cow 432 had an inbreeding coefficient of 38.67. After several unsuccessful matings to her sire 300C, she finally produced a calf, number 484, that lived three days. This calf had an inbreeding coefficient of about 45 per cent. Although bred several times later, she never again became pregnant. She was always negative to agglutination tests. There was no evidence of Trichomoniasis in the herd.

In general the reproductive potential of the dwarf cows was low. Because of complications from Brucellosis and inbreeding, it is difficult to attribute low fecundity to dwarfness *per se*. Despite Brucellosis the non-inbred dwarfs were more fertile than the inbred. The latter were considerably older at first conception even though they were bred as early. Longevity of dwarf cows compares favorably with normal sibs, though the numbers do not warrant definite conclusions.

Lactation Records

Table II summarizes the lactation records for the dwarf cows. With the exception of 406 all the cows were milked three times a day for 305 days. Cow 406 was milked twice a day for 7½ months, when she was purposely turned dry. Standard conversion factors were used to convert her production to three-

times-a-day milking and a lactation period of 305 days.

Cow 460 made a very poor lactation record. The remaining three cows have rather high records when body weight and age are considered. On the whole the dwarfs lactated at a relatively high level.

Is Dwarfism Inherited?

It should be borne in mind that nutrition and management regimes were standardized to a fair degree; dwarfism cannot be attributed to variations from these sources. There remains the possibility of attributing it to disease or pathological conditions during early life. The daily reports of the dairy herdsman fail, however, to show any early pathological condition or illness that might ultimately lead to dwarfism. If dwarfism were caused by some unknown environmental factor, not one offspring of any other sire was affected. It seems logical, therefore, to surmise the existence of a genetic basis.

The data presented in a preceding section show that after one year of age the dwarfs, whether produced by outcrossing or inbreeding, are discontinuous in size with their normal outcrossed or inbred sibs respectively (Figure 17). There is, furthermore, no appreciable difference in size between dwarfs produced by outcrossed or inbred matings. The uniformity of the dwarfs coupled with the small number of animals suggests a monofactorial rather than a multiple-factor type of inheritance. While the genetic data are insufficient to settle the question of inheritance, they are suggestive (Table III). When 300C was bred to his own daughters he produced a total of 12 female progeny; four proved to be normal and two dwarf, while the remaining six died early and are therefore unclassified. If an autosomal recessive

TABLE I. Breeding history of dwarf cows.

Dwarf cows			Calves				
No. and date born	Inbreeding coefficient	Date bred	Sire	Date born	Gestation days	Sex and No.	Fate of calf	Reaction to agglutination test for Brucellosis
349	0.0*	4/18/24	300C	1/24/25	276	♂	Destroyed	
b. 11/1/22		5/24/25	300C	1/18/26	234	♀	Premature lived 1 day	Positive November 11, 1925
		4/26/26	300C	12/18/26	232	♀	Abortion	
406								
b. 1/22/25	0.0*	6/26/26	320A	12/1/26	158	♂	Abortion	Negative up to March 1, 1927;
		2/13/27	300C	11/6/27	263	♀ 488	Lived - Not a dwarf	suspicious March 16, 1927;
								positive June 17, 1927.
460	25.78	pasture bred	347A	5/5/32	?	♀ 519	Lived - Not a dwarf	Negative at all times.
b. 3/24/28		Bred subsequently many times to 347A, but failed to reproduce.						
432	38.67	11/16/28	300C	9/10/29	294	♀ 484	Lived 3 days	Negative at all times
b. 10/5/26		Bred subsequently many times to 300C, but failed to reproduce.						

*The inbreeding coefficient is a fraction of a per cent, but for all practical purposes should be considered 0.

TABLE II. First lactation records of dwarf cows (Semi-official, thrice daily milking).

Cow No.	Age at Freshening Yrs.	Mos.	Lactation days	Milk pounds	Test per cent	Fat pounds
349	2	3	305	7793	5.1	397
406*	1	10		6720	6.0	402
460	4	1	305	3164	5.9	187
432	2	11	305	6840	5.5	375

*Unofficial, 214 days,-converted to thrice-daily milking 305 days.

TABLE III. An analysis of the female progeny sired by 300C.

	Normal	Dwarf	Unclassified Still born or died early	Abortions
	300C X unrelated cows			
Observed	8	2	2	2
	300C X own daughters			
Observed	4	2	4	2
Expected *	5.25	.75		

*On basis of one autosomal recessive gene.

gene is responsible for dwarfism, if sire 300C is heterozygous, and if the maternal grand-dams of the inbred calves are all non-carriers, the expected results from the matings would be seven normals to one dwarf. The observed results for the classified females are in fair agreement with the expectations. If this simple hypothesis of inheritance is tenable for the dwarfs produced by inbreeding, how will it apply to the two dwarfs produced by outcrossing?

In checking over the pedigrees of 300C and the dams of outcrossed dwarfs 349 and 406, one finds two different animals that are common ancestors six to eight generations back.

Concerning the common ancestor that appears more often in all three pedigrees, it was found that sire 300C traces to this ancestor by three different paths. Cow 308, the dam of outcrossed dwarf 349, also traces to this common ancestor by three different paths. The sire of cow 373, the dam of outcrossed dwarf 406, was progeny tested and is a proved non-dwarf carrier. Cow 373 on her maternal side traces, however, to this common ancestor by nine different paths.

The other ancestor that was common to the pedigree of 300C and to the dams of the two outcrossed dwarf calves appears once in two of the pedigrees and twice in the third. Further search might reveal still other common ancestors.

The appearance of these two dwarfs in outcross matings is logical on an autosomal monofactorial recessive basis of inheritance, even though it is not conclusive proof that the recessive monofactorial hypothesis of inheritance is correct.

The progeny resulting from dwarf cows fail to add much information on the inheritance of dwarfism. Most of the calves were born prematurely or died soon after birth before the phenotype could be determined. Dwarf 406 bred to her own sire produced female 488. This calf was kept in the herd six years. She had normal curves for weight, height, and heart girth.

Dwarf 460 produced a female sired by 347A, an inbred son of 300C. The genotype of 347A was never determined. Calf 519 was kept in the herd a year, and all the indices of body size indicated that she was normal. The offspring from these two matings offer additional evidence, which cannot be regarded lightly, that normal size is dominant to dwarfism. All the results appear to fit a monofactorial autosomal recessive type of inheritance.

Discussion

If the condition herein described has been reported before, the fact has escaped the author's attention. These dwarfs should not be confused with the "Duck-legged" cattle described by Lush.[9] In the "Duck-legged" types the long bones of the legs are reduced in length, but the body weight is not appreciably reduced. The "Duck-legged" condition is apparently conditioned by a dominant or incompletely dominant gene that may be identical with the Dexter gene.

These dwarfs are of practical and theoretical interest. In addition to low fecundity, their small size limits their lactating capacity and hence makes them undesirable from the dairyman's standpoint. The line was discarded in 1933 in order to make room for other more desirable lines.

From the standpoint of the inheritance of racial size the dwarfs are of considerable interest. Although the evidence is inconclusive, it seems logical to suspect that one factor pair conditions this type of proportionate dwarfism. If this interpretation is correct, one pair of size factors has been observed and isolated from the multiple factor complex regulating racial size in cattle.

Physiological and endocrine relationships of the dwarfs are not without interest, but studies of that nature were not possible when the animals were available.

Summary

A new type of proportionate dwarfism segregated from inbred and outcross matings among the progeny of one sire. At birth the dwarfs cannot be

distinguished by appearance, weight, height, or heart girth. Though they grow more slowly than normal outcrossed or inbred sibs, they cannot be identified until about 12 months old.

All the dwarfs reproduced, but on the whole their reproductive potential was lower than that of normal outcrossed or inbred sibs. Considering body size and age, three of them lactated rather well; the fourth very poorly.

The evidence indicates that this particular type of dwarfism is hereditary and may be conditioned by a single autosomal recessive gene.

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✦

LAY OPINIONS ABOUT EUGENICS

After reading a paper by S. J. Holmes on "The Opposition to Eugenics" (*Science* 89:351-357. April 21, 1939), the students in my eugenics class became interested in testing the reaction of residents of Houston, Texas, to eugenics. A questionnaire was prepared, made up of seven major questions comprising a total of forty specific items regarding various eugenic problems. This was presented by interviewers to a hundred residents of Houston. The responses were tabulated and an attempt was made to relate these answers to the religious, professional, marital status, and age of the respondents. In general we are probably justified in stating that while the group questioned was not particularly enthusiastic about eugenics, at least a large majority held good eugenic opinions and would not oppose an eugenic program. There were definite religious differences in reaction.

A detailed report of this study, with a tabulation of the replies has been filed with the American Documentation Institution as Document Number 1654. Copies can be obtained from the nonprofit Bibliofilm Service, 1719 N St., N. W., Washington, D. C., by ordering Document 1654, remitting 25 cents for copy in microfilm, readably enlarged full-size on reading machine or hand viewer, or $1.60 for copy in the form of paper photoprints readable without optical aid.

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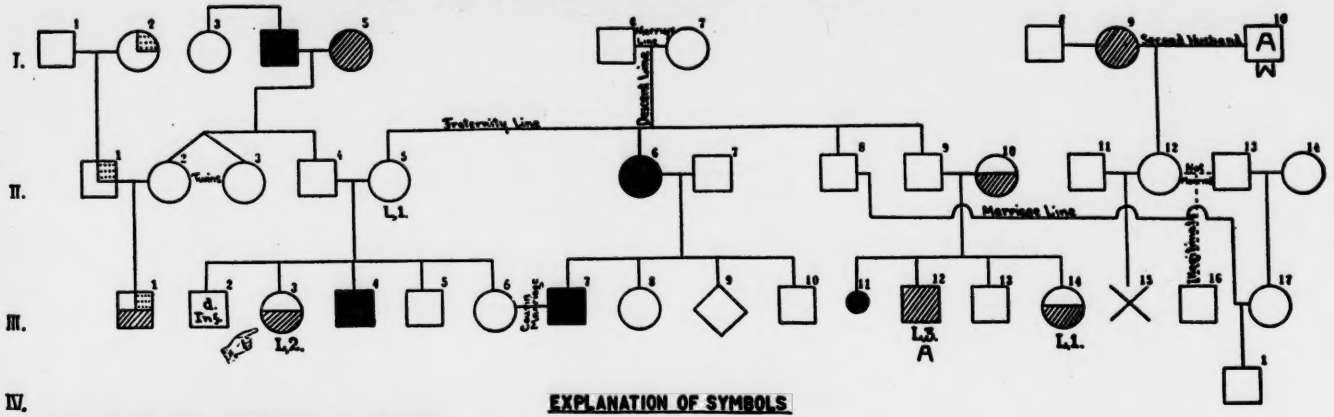

EXPLANATION OF SYMBOLS

(a) **Standard for all Pedigree Charts:**

□=Male; ○=Female; ◇=Sex unknown; ●=Still-birth or Miscarriage; X=Children — number and sex unknown; ○○=Twins; d. Inf.=Died in Infancy; ☞ Points to the Propositus or central figure in the pedigree.

□—○=Parents.

□○□○○=Children.

Roman figures to the left indicate generations; Arabic figures locate individuals, (thus III. 7 is the young man in the third generation who married his cousin).

The following letters, placed in or around the individual's pedigree symbol, are standard for certain traits: A, alcoholic; B, blind; D, deaf; E, epileptic, F, feebleminded; I, insane, M, migraineous; N, normal in reference to traits under consideration; Ne, neurotic; P, paralytic; Sx, sexually immoral; S, syphilitic; T, tuberculous; W, wanderer.

(b) **Especially devised or selected for this particular pedigree-chart:**

■ ● = Successful leaders in politics. ◪ ◔ = Extra thumb on right hand. L.1. = Highly successful author. L.3. = Little or no ability in literary efforts. ▨ ◍ = Superior in vocal music. ▨ ◍ = Medium attainment in vocal music.

To fit the particular family and traits (whether physical, mental or temperamental; good or bad) under consideration, invent special symbols, or select special letters (in addition to those standardized under (a) above) to be placed within or near the particular individual's pedigree symbol, to indicate particular traits and their degree of development.

Prepared by the International Commission of Eugenics. See *Journal of Heredity* for August 1926. Additional copies may be obtained from A.G.A.